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NATIONAL MUSEUM OF VICTORIA

# RECORDS

# OF THE

# AUSTRALIAN MUSEUM

NATIONAL MUSEUM
26 SEP 1983
OF VICTORIA

## VOL. 33

THE AUSTRALIAN MUSEUM
SYDNEY, 1980-1981

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# A REVIEW OF THE GENERA OF THE CINGULOPSIDAE WITH A REVISION OF THE AUSTRALIAN AND TROPICAL INDO-PACIFIC SPECIES (MOLLUSCA: GASTROPODA: PROSOBRANCHIA)

NATIONAL MUSEUM
22 APR 1981
OF VICTORIA

W. F. PONDER AND E. K. YOO

The Australian Museum

This paper is dedicated to Jacques Voorwinde.

## SUMMARY

The genera of the Cingulopsidae (= Coriandriidae Nordsieck and Eatoninidae Golikov & Starobogatov) are reviewed and 30 species and subspecies are described from Australia and the tropical Indo-West Pacific, 24 of them new. Four genera are recognised in the family. *Eatonina* Thiele, 1912 has 5 subgenera; *Eatonina* s.s. (= *Saginofusca* Ponder, 1965) with 15 species and subspecies, *Coriandria* Tomlin, 1917 (= *Cingulopsis* Fretter & Patil, 1958 and probably *Globisetia* Nordsieck, 1972) with 2 species, *Otatara* Ponder, 1965 and *Mistostigma* Berry, 1947 with no Australian species and *Captitonia* nov. with 1 species. *Eatoniopsis* Thiele, 1912 has 4 subgenera; *Eatoniopsis* s.s. with no Australian species, *Boogina* Thiele, 1913 with 1 species, *Rufodardanula* Ponder, 1965 with 2 species and *Pilitonia* nov. with 2 species. *Tubbreva* Ponder, 1965 contains 2 species and *Pseudopisinna* nov. has 4 species and 1 subspecies.

The family Cingulopsidae has not previously been recognised from Australia, the named species having formerly been included in the Rissoidae.

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## INTRODUCTION

The family Cingulopsidae is a group of minute prosobranch gastropods in the superfamily Rissoacea. They live in shallow seas throughout the world and are sometimes relatively abundant components of the algal-living micro-mollusc fauna. The family name was introduced as recently as 1958 by Fretter and Patil on anatomical evidence. Their work was based on a minute, common British species which had previously been placed in the Rissoidae under a variety of generic names and for which they created the name *Cingulopsis*. The Cingulopsidae has not previously been recognised from Australia, the few described species shown herein to be cingulopsids have been included in the Rissoidae.

Members of the Cingulopsidae have a number of distinct anatomical characters which separate them from the Rissoidae and the Eatoniellidae, although the shell forms in all three families are very similar. It was only from studies on the radulae, opercula and anatomy that the family could be properly delineated.

The two earliest valid generic names given to cingulopsids, *Eatonina* and *Eatoniopsis*, date from Thiele's (1912) work on Antarctic and Subantarctic molluscs. A third genus name based on a cingulopsid, *Watsoniella*, proved to be a homonym which Thiele later (1913) replaced with *Boogina*. *Eatonina* was actually based on a South African species. Thiele regarded these three genera as members of the Rissoidae.

Coan (1964) in his review of the genera of the Rissoidae, Rissoinidae and Cingulopsidae included *Coriandria* Tomlin, 1917 in the last family as a possible additional genus on shell characters. Ponder (1965a) introduced a new genus name and 3 new subgenera for New Zealand species, recognised Thiele's southern genera as cingulopsids, and split the family into 2 subfamilies. Ponder (1968) described the anatomy of a New Zealand cingulopsid, *Eatonina micans* (Webster). Nordsieck (1972) placed *Cingulopsis* as a synonym of *Coriandria*, and unnecessarily introduced Coriandriidae to replace Cingulopsidae (see International Code on Zoological Nomenclature, Article 40). He also included *Rudolphosetia* Monterosato in the family, following Wenz (1943), who regarded *Coriandria* as a synonym of *Rudolphosetia*.

Fretter and Patil (1958) placed the Cingulopsidae tentatively in the Rissoacea, but Golikov and Starobogatov (1975) included it in a new superfamily grouping Trachysmatoidea along with a new family Eatoninidae. The Eatoninidae was erected solely on the basis of a more conical shell and the "absence of a second pallial duct connecting the distal end of the renal gonoduct with the mantle cavity". In view of the close similarity in all other features of *Coriandria (=Cingulopsis)* and *Eatonina* (we believe them to be congeneric) the family name Eatoninidae is, in our opinion, unwarranted.

Ponder (1965a) introduced a subfamily Eatoniopsinae for species with a smaller opercular peg, different radular characters and a relatively larger stomach. However, no species of the group as recognised by Ponder (1965a) (*Eatoniopsis* Thiele, 1912, *Boogina* Thiele, 1913, *Rufodardanula* Ponder, 1965 and *Tubbreva* Ponder, 1965) has been fully investigated anatomically, and because of the general similarity in shell, radula and operculum to typical members of the Cingulopsidae, we are not retaining this subfamilial division here.

The family Cingulopsidae appears to be centred in the Southern Hemisphere where the majority of known species are located. Little is known of the fossil history of this family because few fossil cingulopsids can be identified with certainty owing to the lack of definitive shell characters. *Eatonina (Mistostigma) punctulum* Berry (=*albida* Carpenter) occurs in the Pliocene of California and *Pseudopisinna* (gen. nov.) *gregaria* (Laseron) is known from the Pliocene of Bass Strait, Australia.

## MATERIALS AND METHODS

The methods used are described by Ponder & Yoo (1977). All material, unless otherwise noted, is housed in the Australian Museum, Sydney. The number of specimens examined is indicated in brackets after each locality.

## ABBREVIATIONS

| | |
|---|---|
| AM | Australian Museum, Sydney. |
| ANSP | Academy of Natural Sciences of Philadelphia, Philadelphia. |
| BMNH | British Museum (Natural History), London. |
| coll. | collected by. |
| Coll. | collection. |
| NMV | National Museum of Victoria, Melbourne. |
| NMNH | National Museum of Natural History, Washington D.C. |
| N.S.W. | New South Wales. |
| Qld | Queensland. |
| QM | Queensland Museum, Brisbane. |
| S.A. | South Australia. |
| SAM | South Australian Museum, Adelaide. |
| SEM | Scanning Electron Microscope. |
| sev | several. |
| S.W.A. | South Western Australia. |
| Tasm. | Tasmania. |
| TM | Tasmanian Museum, Hobart. |
| Vic. | Victoria. |
| W.A. | Western Australia. |
| WAM | Western Australian Museum, Perth. |
| w | used in 'material examined' to indicate the number of 'wet' (i.e. formalin preserved) specimens. |

Note: In the locality data, and sometimes elsewhere, compass points (north, south, etc.) are abbreviated to N., S. etc.

## TAXONOMY

### Family **Cingulopsidae** Fretter & Patil, 1958.

Synonyms Eatoniopsinae Ponder, 1965.
Coriandriidae Nordsieck, 1972.
Eatoninidae Golikov & Starobogatov, 1975.

DIAGNOSIS. Shell minute, pupoid to depressed trochiform, umbilicate to nonumbilicate, smooth or with spiral or axial sculpture. Aperture simple, lacking a varix. Protoconch paucispiral, almost smooth, with no true sculpture. Operculum paucispiral, oval, transparent, horny, with a peg arising from the nucleus on the inner surface. Radula taenioglossan; central teeth with small to obsolete cusps; lateral teeth large; inner marginal teeth long, with prominent cusps; outer marginal teeth of moderate size and hook-like or short and triangular. Radula absent in one genus (*Tubbreva*). Headfoot unpigmented or orange to orange-red in colour. Head with a pair of simple, rather short to long tentacles with eyes in bulges at their outer bases, and a bilobed snout. Foot simple, with longitudinal mucous slit in metapodial portion of sole, anterior mucous gland opens supramarginally. Metapodial and pallial tentacles absent. Jaws absent. Oesophageal gland present, crystalline style and style sac absent, intestine short and lacking typhlosoles. Circumoesophageal ganglia concentrated. Renal organ simple. Sexes separate, genital ducts closed, male aphallate, female pallial duct monaulic or diaulic (Fretter & Patil, 1958; Ponder, 1968). Eggs laid singly in capsules, no free larval stage in development (Lebour, 1937; Fretter & Patil, 1958).

RELATIONSHIP WITH OTHER FAMILIES. The Cingulopsidae are very similar to some genera of the Rissoidae, Eatoniellidae and Rastodentidae in having smooth, simple, conical shells. A similarly pegged operculum also occurs in these three families (Eatoniellidae (Ponder, 1965c), Rastodentidae (Ponder, 1965b), some Rissoidae (e.g. *Barleeia, Rissoina, Fictonoba* (Ponder, 1967). All of these groups can, however, be readily distinguished on radular characters and are very distinct anatomically (Ponder, 1968) from the two species of Cingulopsidae so far investigated.

## KEY TO GENERA

1. Shell ovate, elongate-conical, ovate-conical, to depressed trochiform, aperture subcircular to circular with narrow inner lip, smooth or with spiral striae or spiral keels; central teeth of radula moderately large to small, each lateral tooth without a long inner extension, or radula absent .................................... 2

   Shell pupoid, aperture circular with broad inner lip, smooth or with axial sculpture; central teeth of radula relatively minute, each lateral tooth with long inner extension .............................................................*Pseudopisinna*

2. Aperture of shell subcircular to circular, with simple, concave columella; operculum usually with internal longitudinal ridge..................................*Eatonina*

   Aperture of shell subcircular, with columella more or less straight (vertical) and bearing a weak bulge; operculum without internal ridge............................ 3

3. Shell ovate-conical to depressed-trochiform; operculum with peg projecting beyond margin; radula present ...................................................*Eatoniopsis*

   Shell elongate-conical; operculum with peg not projecting beyond margin; radula absent ....................................................................*Tubbreva*

## Genus **Eatonina** Thiele, 1912:279.

Type species (original designation): *Eatoniella (Eatonina) pusilla* Thiele, 1912: 279.

DIAGNOSIS. Shell minute, ovate-conical to ovate, nonumbilicate to narrowly umbilicate, smooth except for axial growth lines and (usually) indistinct spiral grooves, or with spiral keels, with rounded body whorl and weakly to strongly convex spire whorls. Protoconch dome-shaped, smooth, of less than 2 whorls. Aperture subcircular to circular, inner lip rather narrow to moderately broad, merging with the weakly and evenly concave columella. Operculum thick, yellowish, transparent, usually with longitudinal, internal ridge; peg strong, straight, short, usually grooved. Radula with moderate-sized central teeth each bearing small to minute cusps on cutting edge, with lateral fold-like thickenings and with or without denticles on inner-face. Lateral teeth large, approximately rectangular to nearly triangular, cutting edge long, straight or weakly curved, with 1 to many cusps, often 1-3 larger than rest. Inner marginal teeth each curved, simple except for large cusps on distal cutting edge and usually with 1-2 peg-like protuberances (supporting structures) projecting from proximal half of tooth on which outer marginal tooth rests. Outer marginal teeth short, uni to multicuspate, with relatively broad bases. Headfoot and anatomy as in family diagnosis.

DISTRIBUTION. South Africa, west coasts of North and South America, New Zealand, Australia and the tropical Indo-Pacific.

REMARKS. Genus-group taxa which appear to be congeneric with *Eatonina* are *Coriandria* Tomlin, 1917, *Cingulopsis* Fretter and Patil, 1958, *Globisetia* Nordsieck, 1972 (all here regarded as forming one subgenus), *Otatara* Ponder, 1965 and *Mistostigma* Berry, 1947. The anatomy of *Coriandria (=Cingulopsis) fulgida* is very similar to that of *Eatonina micans* (Fretter & Patil, 1958; Ponder, 1968) although it differs in a few details, notably in *C. fulgida* having a ciliated accessory pallial duct in the female reproductive system, and a more complex osphradium. In view of the similarity in shell, radular, and opercular characters, the anatomical differences are considered here to be of subgeneric importance only. In our opinion further species need to be investigated anatomically before the significance of the anatomical differences can be fully assessed. Fretter and Patil (1958) described a short metapodial tentacle in *C. fulgida* but examination of living material of that species and of several other species in the family has indicated that there is not a true tentacle present but merely the posterior part of the opercular lobe which sometimes projects very slightly beyond the posterior edge of the operculum.

The tropical species of this genus have, with two exceptions, a rather complex colour pattern unlike the uniform coloration of most of the Australian temperate species. This characteristic is not, however, associated with parallel peculiarities in radular or shell features.

*Eatonina* was introduced by Thiele for a new species *(pusilla)* from Simons Bay, South Africa. The type specimen is, unfortunately, totally destroyed by corrosion and one of us (W.F.P.) could not locate any other author's material in the Humbolt-Universität Museum, although Thiele stated that several specimens existed in the original lot. Thiele's original figures and description, however, allows *E. pusilla* to be recognised with reasonable certainty and it appears to be synonymous with *Barleeia smithi* Bartsch, 1915. Specimens assumed to be *E. pusilla* were made available by Mrs E. Connolly and the shell, radula and operculum are figured for comparison with Australian species (figs 14j-m). A New Zealand species placed in *Eatonina* by Ponder (1965a), *E. micans* (Webster 1905), agrees well with the type of the genus in radular, shell and opercular features and can be taken as being typical. This species has been described anatomically by Ponder (1968).

*Saginofusca* Ponder was introduced as a subgenus of *Eatonina* for two New Zealand species (Ponder, 1965a) and one species was later named under this subgenus from Chile (Marincovich, 1973). The subgenus was chiefly characterised by a rather globose, umbilicate shell and multicuspate lateral teeth (figs 14d-g). Examination of the Australian fauna leads us to the view that *Saginofusca* cannot be usefully distinguished from *Eatonina s.s.* when the subgenus is considered in a broader context. Most species show some secondary cusps on the lateral teeth and some with multicuspate lateral teeth are ovate-conical and nonumbilicate. In other respects *Saginofusca* is like *Eatonina.*

The denticles on the inner face of the central teeth of species of this subgenus are useful in species determination as they appear to be consistent within a species. All gradations between 2 pairs of large denticles, a single pair of denticles and no denticles are found among the various species. Thus the presence or absence of denticles cannot be used alone as a taxonomic character at the subgeneric level. The hump-like inner, upper edge of the lateral teeth is characteristic of the subgenus, although in some species (e.g. *sanguinolenta* nov.) this hump is only weakly developed. The cusp patterns on the lateral and marginal teeth show much greater diversity than in the subgenus *Coriandria* and whereas there is some minor intraspecific variation, they are generally useful in separating the species.

The radulae of species of *Eatonina* can be grouped into 3 main types (fig. 1). The first group, and perhaps the most primitive, is exhibited by the type species of the subgenus *Mistostigma (albida)*. The central teeth each have 3 prominent cusps (the median one the smallest) and 4 denticles on the face. The lateral margins of each central tooth are only slightly thickened. The lateral teeth have 3 large cusps and a fourth small cusp, an evenly convex upper margin and two weak denticles on the face. The radulae of species in the remainder of the genus can be derived from this type by the loss or modification of various structures. A Chilean species, *E. atacamae* Marincovich, 1973 shows a radula which presents some intermediate features between the type species of *Mistostigma* and species included in *Eatonina* s.s. It has weak denticles on the face of each lateral tooth and the dorsal margin of this tooth has developed a weak hump near its inner edge, although the 4 cusps are all approximately equal in size. The central teeth have apparently lost the median cusp and this appears to have been replaced by a low denticle on the upper margin, and the lateral cusps are reduced to weak denticles. Perhaps to compensate for this reduction in cusps the 4 denticles on the face of each central tooth have become large and cusp-like and the lateral thickenings have also developed a cusp-like appearance and become separated from part of the lower margins of the tooth. Three southern Australasian species of *Eatonina (rubrilabiata* nov., *shirleyae* nov. and *atomaria* (Powell)) have a radula which may have been derived from the type seen in *E. atacamae* by a strengthening of the lateral folds of the central teeth, and, in the lateral teeth, the loss of the denticles on the face, an increase in the development of the hump on the dorsal margin and, perhaps associated with this, a corresponding disparity in the development of the cusps.

Further evolution within the subgenus *Eatonina* appears to have resulted in a greater development of the lateral folds of the central teeth to a point where these structures apparently take over the function of cusps, with a resultant decrease in the size of the "pseudo-cusps" or denticles on the face of these teeth. A progressive series demonstrating this is seen in 3 groups of species. In the first group *(micans* (Webster), *hutchingsae* nov. (figs 1, 10b, f), *hedleyi* nov. (fig. 10l) and *capricornea* (Hedley) (figs 8i, j)), there are 4 weak to moderate denticles on the face of the central teeth, but in the second group the outer pair of denticles is absent and has presumably been lost *(pusilla* (Thiele) (fig. 14m), *pulicaria* (Fischer) (figs 1, 7h, j), *lunata* (Laseron) (fig. 8e), *heliciformis* nov. (fig. 10i) and *ardeae* nov. (fig. 6d)). The loss of the remaining paired denticles would give rise to the last group *(colorata* nov. (figs 1, 7e) and *striata* nov. (figs 1, 9l)). The type species of the new subgenus *Captitonia (lirata* nov.*)* has a radula which also falls into this latter group (figs 1, 15m) and is presumably derived from a species such as *striata* nov. The third type of radula occurs in the subgenus *Coriandria.* It has a central tooth which may have been derived from a *Mistostigma*-like ancestor by the loss of the denticles on the face of the tooth, the development of the lateral folds and a retention of a pair of cusps (Fig. 1). The lateral teeth are essentially like those of *Mistostigma* but have one of the denticles on the face of these teeth, whereas there is a pair in *Mistostigma.*

Three species *(sanguinolenta* nov. (figs 1, 9i, j), *lactea* nov. (figs 1, 8n, o) and *condita* nov. (figs 1, 9e)) appear to fall between *Eatonina* s.s. and *Coriandria* in radular features. Two *(lactea, sanguinolenta)* lack any denticles on the face of the central teeth and one *(condita)* has 2 very weak denticles. The lateral teeth in *lactea* and *sanguinolenta* are multicuspate and the cusps show a reasonable amount of disparity in size. The dorsal margin of the lateral teeth has only a weak hump giving an outline more similar to that seen in *Coriandria* than in *Eatonina* s.s. One species *(lactea)* has a shell almost identical to that of *E. pulicaria* and the radula could have been derived from that species by a reduction in the dorsal hump on the lateral teeth with associated greater uniformity of the cusps. A fusion of the upper ends of the lateral folds of the central teeth to form a continuous structure dorsally and laterally and a loss (?) of the denticles on the face would result in the type of central tooth observed in *E. lactea.* In *E. sanguinolenta* the face of the central tooth has been thickened, possibly by fusion and spreading of the denticles. The lateral teeth are weakly humped and there is little discrepancy in the size of the cusps. In shell features this species resembles several species here placed in *Eatonina* s.s. The third species, *E. condita,* has very weak denticles on the face of the central teeth and has almost no hump on the lateral teeth. This species is very similar to *E. sanguinolenta* in shell and radular features and they are probably closely related. Another interpretation of the observed radular features in these 3 discordant species is that they form a separate group which arose independently from a *Mistostigma*-like ancestor. There is, however, little supportive evidence for this view other than the common feature of the evenly convex dorsal outline of the lateral teeth. In fact the available evidence suggests that the radula observed in *E. lactea* developed quite independently from that of *E. condita* and *E. sanguinolenta.*

The radula of the subgenus *Otatara* has not been re-examined using the SEM and, consequently, its relationships with *Eatonina* s.s. are difficult to assess. The available information suggests that the radula of *E. (Otatara) subflavescens* (Iredale) has been derived from a typical *Eatonina* radula by reduction of the cusps to one on all teeth.

## KEY TO SUBGENERA OF *EATONINA.*

1. Shell with smooth or with weakly spirally striate surface and sometimes a sutural cord .......... 2
   Shell with heavy spiral keels .......... *Captitonia*
2. Outer marginal teeth each with a single cusp .......... *Otatara*
   Outer marginal teeth each with 2 or more cusps .......... 3
3. Central teeth of radula with conspicuous cusps on cutting edge .......... 4
   Central teeth of radula with very inconspicuous denticle-like cusps on cutting edge or 1 short median cusp .......... *Eatonina* s.s.

4. Central teeth of radula with 1-2 blunt cusps on cutting edge and no denticles on its inner face .......... *Coriandria*

Central teeth of radula with 3 cusps on cutting edge and with denticles on inner face .......... *Mistostigma*

## KEY TO THE AUSTRALIAN AND TROPICAL INDO-PACIFIC SPECIES OF EATONINA.

This key will have a reasonable reliability when used with live-collected adults and preferably with more than one specimen. Because of the simplicity of the shells and the subtle nature of the differences separating the species any identification made on shell characters alone must always have an element of doubt.

1. Shell with distinct dense-white blotches or bands .......... 2

Shell more-or-less uniformly coloured .......... 7

2. Shell greater than 1.7 mm in length .......... *E. (E.) lunata* (Laseron)

Shell less than 1.6 mm in length .......... 3

3. Shell ovate-conical or conical .......... 4

Shell depressed-ovate .......... *E. (E.) heliciformis* nov.

4. Shell with distinct brown and white bands .......... 6

Shell with brown and/or white markings not arranged in simple bands .......... 5

5. Shell with ground colour (dark brown) arranged in a single spiral series of dark rectangles or spots adapical to periphery .......... *E. (E.) pulicaria* (Fischer)

Shell with ground colour (colourless to brown) arranged in two spiral series of irregular markings adapical to periphery .......... *E. (E.) lactea* nov.

6. Shell with the white bands made up of alternating dense-white and colourless patches .......... *E. (E.) colorata* nov.

Shell with simple white bands .......... *E. (E.) ardeae* nov.

7. Shell smooth or finely spirally striate .......... 8

Shell spirally carinate .......... *E. (Captitonia) lirata* nov.

8. Shell with weak sutural cord and distinct spiral striae .......... *E. (E.) striata* nov.

Shell smooth or with indistinct spiral striae .......... 9

9. Shell distinctly umbilicate .......... 10

Shell not distinctly umbilicate (but sometimes with a very narrow umbilicus or umbilical chink) .......... 11

10. Shell ovate conical .......... *E. (E.) capricornea* (Hedley)

Shell broadly ovate .......... *E. (E.) hedleyi* nov.

11. Shell with inner lip very much darker than rest of shell .......... 12

Shell with inner lip slightly or not darker than rest of shell .......... 17

12. Shell orange or red-brown .......... 13

Shell pale yellow or yellow-brown ..........*E. (Coriandria) fulvicolumella* nov.

13. Shell broadly ovate-conic, outer lip prosocline .......... 14

Shell narrowly ovate-conic to conical, outer lip prosocline to orthocline.......... 15

14. Shell medium orange-brown ..........*E. (E.) hutchingsae* nov.

Shell dark red-brown..........*E. (Coriandria) rubicunda* nov.

15. Shell with very distinct dark red-brown false-margined sutures .......... *E. (E.) sanguinolenta* nov.

Shell lacking distinct darker sutural band.......... 16

16. Shell ovate-conic..........*E. (E.) rubrilabiata* nov.

Shell conical ..........*E. (E.) condita* nov.

17. Shell ovate-conic .......... 18

Shell conical ..........*E. (E.) ardeae* nov.

18. Shell with distinctly convex whorls, outer lip weakly prosocline, surface almost smooth ..........*E. (Coriandria) rubicunda* nov.

Shell with weakly convex whorls, outer lip distinctly prosocline, surface with very fine spiral striae..........*E. (E.) shirleyae* nov.

## Subgenus **Eatonina** s.s.

Synonym *Saginofusca* Ponder, 1965a: 121.

Type species (original designation): *Notosetia atomaria* Powell, 1933.

DIAGNOSIS. Shell as for genus, smooth except for growth lines, or rarely very weak axial riblets and sometimes spiral striae. A sutural cord rarely present. Usually unicoloured, most species coloured various shades of brown, sometimes spotted. Operculum as for genus. Radula with each central tooth having 0-2 pairs of conspicuous denticles on its inner face and very small denticle-like processes on its cutting edge; lateral teeth large, subrectangular, with few to many cusps, usually 1-3 cusps predominant, inner upper edge raised into a moderate to strong hump; each inner marginal tooth elongate, with few long cusps distally, a conspicuous cusp-like swelling about half way along its length on which outer marginal tooth rests; outer marginal teeth short, with wide bases and with 3 or more cusps. Head-foot as in family diagnosis, female genital duct monaulic.

DISTRIBUTION. Australasia, tropical Indo-Pacific and South Africa (fig. 18).

REMARKS. The shells of the species placed in this subgenus vary considerably in size, colour and shape but the overall similarity of their radular features suggests that they are probably a natural group.

### **Eatonina (Eatonina) ardeae** sp. nov.

Figs 2b, c; 6a-d

Derivation of name: *ardea* (Latin) = heron, named for Heron Is., Qld.

DESCRIPTION. *Shell.* Minute, conical, solid, smooth except for very fine spiral striae, non-umbilicate, dark orange brown to chocolate-brown, some with white spiral bands. Protoconch of 1½ whorls; teleoconch of 2¼-3 very lightly convex whorls, smooth except for extremely fine spiral striae (rather distinct in holotype, indistinct in some other specimens) and indistinct growth lines. Aperture subcircular, with narrow inner lip, abapical portion raised as a thin lamella from base; outer lip thin, weakly prosocline, sharply bent abapically at suture. Colour dark orange-brown to chocolate brown, a darker band abapical to suture (false margined rather than a true colour band). Some specimens with a creamy white band on penultimate and body whorls encompassing most of abapical half of each whorl and a second faint band usually present on base. Free part of inner lip and outer lip yellowish-brown. A zig-zag or simple vertical white streak about ⅛-¼ whorl abapertural to outer lip in some specimens (including holotype), absent in others.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.02 mm | 0.64 mm |
| Paratype | 0.96 mm | 0.65 mm |
| Paratype | 1.04 mm | 0.68 mm |
| Figured specimens | | |
| Paratype (SEM stub 476) | 1.16 mm | 0.73 mm |
| Heron Is., Qld (SEM stub no. 490) (banded specimen) | 1.12 mm | 0.68 mm |
| Heron Is., Qld (banded specimen) | 1.00 mm | 0.66 mm |
| Heron Is., Qld (large banded specimen) | 1.32 mm | 0.82 mm |

*Operculum.* Typical of genus (fig. 6c).

*Radula.* Typical of subgenus; central tooth with a pair of long denticles on inner face; a rudimentary denticle below upper edge; lateral folds long, curved ventrally. Lateral teeth with low swelling on upper inner edge; 5-6 comb-like cusps on inner side of large, blunt, main cusp and 2 small, blunt cusps on outer side. Inner marginal teeth with 4 cusps, third about twice as large as the others. Outer marginal teeth with 6 rather short, sharp cusps (fig. 6d).

Opercula and radulae examined from type locality (stub no. 476) and Heron Is., Qld, same data as last except 8 m, 27 Dec., 1976 (banded form) (SEM stub no. 490).

*Head-foot.* Translucent white, odontophore orange, snout pale orange.

TYPES. Holotype (C. 106169) and 2 paratypes (C. 106170), 3 paratypes (C. 106171), AM; 1 paratype (MO 6313), QM; 1 shell, 1 operculum and 1 radula (SEM stub no. 476).

TYPE LOCALITY. S. side of Heron Is., Qld, opposite Research Station, over reef edge, 2 m, in coral rubble with algal coating, 26 Dec., 1976, coll. W. F. Ponder.

ADDITIONAL LOCALITY FOR PARATYPES. Heron Is., Qld, 26 m, J. Voorwinde Coll. (C. 106171).

ADDITIONAL MATERIAL EXAMINED. *Qld:* S. side of Heron Is., 8m in coral rubble with algal coating, over reef edge (12/2w). S.E. of Heron Is. 6m (3). Heron Is. 4m (1); 11m (1).

DISTRIBUTION AND HABITAT. Known only from Heron Is., Queensland, in the sublittoral living in coral rubble with algae (fig. 19).

REMARKS. This species is similar in general appearance to some of the southern *Eatonina* species but differs in its evenly conical form, dimorphic colour pattern and radular features. The radulae of the 2 colour forms are identical but the colour pattern does not appear to intergrade in the material available, suggesting that it may be a genetically based colour dimorphism.

### **Eatonina (Eatonina) capricornea** (Hedley, 1907)

Figs 2a; 8f-j

*Amphithalamus capricorneus* Hedley, 1907: 495, pl. 17, fig. 22.

*Scrobs capricorneus.* — Cotton, 1944: 311.

*Lucidestea capricornea.* — Laseron, 1956: 450, fig. 174.

DESCRIPTION. *Shell.* Minute, ovate-conical, solid, opaque to subopaque, smooth, very narrowly to narrowly umbilicate, yellowish to orange-brown, sometimes banded. Protoconch of 1¾ smooth whorls, teleoconch of 2¼-2½ moderately convex whorls, smooth and shining except for weak growth lines and very indistinct spiral scratches. Aperture subcircular, to almost pyriform; inner lip narrow, its edge nearly straight, abapical portion a thin lamella separated from base; outer lip thin, its edge orthocline. Suture slightly inclined abapically just abaperturally to outer lip. Colour yellowish-white to orange-brown, paler shells sometimes with 2 rather indistinct pale brown bands, one on middle base, the other between suture and periphery of body whorl; umbilical area and inner lip usually orange-brown.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.54 mm | 1.05 mm |
| Figured specimens | | |
| Paratypes (SEM stub no. 445) | 1.55 mm | 1.00 mm |
| | 1.44 mm | 0.90 mm |

*Operculum.* Typical (fig. 8h).

*Radula.* Typical of subgenus; central tooth with a pair of very weak denticles on inner face; low, triangular swelling on upper edge with convex cutting edge below; lateral folds broad, almost straight. Lateral teeth with massive, knob-like swelling on upper inner edge which fits socket formed by large, sharp triangular cusp and cusp-like protrusion on inner side; 2 small cusps on median part of cutting edge. Inner marginal teeth with 3 sharp cusps, middle one longest, inner edge near base with weak serrations. Outer marginal teeth small, with 3 short cusps (figs 8i, j).

Opercula and radulae examined from type locality (SEM stub nos, 444, 445) and operculum from Port Denison, Bowen, Qld (SEM stub no. 446).

TYPES. Holotype (C. 19354) and many paratypes (C. 106276), AM; 2 paratypes (MO 6315), QM; 2 shells, 3 opercula and 3 radulae (SEM stub nos 444,445).

TYPE LOCALITY. Masthead Is., Capricorn Group, Qld, 31-36 m, coll. C. Hedley.

ADDITIONAL MATERIAL EXAMINED. *Qld:* Port Denison, Bowen, dredged (8). Shoal

Point, Mackay, on reef at low tide (25). Sarina Beach, S. of Mackay (1). 3 km N.E. of W. side of Gillet Cay, Swains Reef, 64-73 m (27). 5.6 km W. of North Keppel Is., Keppel Bay (1). N.E. of Rockhampton, 64 m (1).

DISTRIBUTION AND HABITAT. Bowen to the Capricorn Group, Queensland, from low water to about 70 m. The only material available that was collected alive includes a few dredged off Bowen and at Masthead Island. In both cases the details of the substrate are not known but was probably coral sand and algae (fig. 19).

REMARKS. The radulae of specimens with shells representing the two extremes of colour have been examined and found to be identical. There is a little variation in the relative height of the spire amongst the extensive paratype series, but otherwise the species appears to be very uniform in shape.

The shell of this species differs from the common tropical species *Eatonina (Eatonina) lunata* in colour and shape. It is somewhat similar to some of the species from temperate Australia but differs in sometimes having a colour pattern and in the presence of a narrow umbilicus as well as in radular features.

### **Eatonina (Eatonina) colorata** sp. nov.

Figs 3a; 7a-e

Derivation of name: *coloratus* (Latin) = coloured.

DESCRIPTION. *Shell.* Minute, solid, conical, nonumbilicate, brown and white, with brown bands on body whorl. Protoconch of 1½ whorls; teleoconch of 2½, very weakly convex whorls, smooth except for weak prosocline growth lines and very indistinct spiral scratches. Aperture subcircular, inner lip narrow, its edge distinctly concave, adapical portion hardly separated from base; outer lip rather strongly prosocline. Suture bent a little adapically just abaperturally to outer lip. Umbilical chink minute or absent, no umbilicus. Colour dark brown, protoconch and first whorl of teleoconch a little paler than rest of shell; a white band on about abapical ⅔ of all whorls to last 1½ whorls of teleoconch, last ½ of penultimate whorl with narrow brown band adapical to suture as well as one abapical to suture; base with a narrow white band in middle; all bands clearly visible within aperture; inner lip dark brown. White bands made up of close-set, dense white blotches usually alternating with vertical, narrow, translucent, colourless patches.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 0.88 mm | 0.60 mm |
| Paratype | 0.86 mm | 0.60 mm |
| Figured specimen | | |
| Paratype (SEM stub no. 138) | 0.90 mm | 0.62 mm |

*Operculum.* Typical (figs 7b, c).

*Radula.* All but central teeth typical of subgenus; central tooth with prominent, vertical, lateral folds and a narrow, vertical median thickening; no other structures apparent. Lateral teeth with a low swelling on upper inner edge; 5 comb-like cusps on inner side of large, blunt main cusp and 3 small cusps on outer side. Inner marginal teeth with 7 cusps spread evenly along most of the tooth, second cusp slightly longer than others. Outer marginal teeth with 3 short cusps (figs 7d, e).

Opercula and radulae examined from type locality (SEM stub no. 479).

TYPES. Holotype (C. 106193) and 28/3w paratypes (C. 106194), AM; 1 shell (SEM stub no. 138) and 1 shell, 2 opercula and 2 radulae (SEM stub no. 479).

TYPE LOCALITY. Pt. Ardel, Port Vila, Efate, New Hebrides, coral block washings, low tide, Jan. 16, 1967, coll. W. F. Ponder.

ADDITIONAL MATERIAL EXAMINED. *New Hebrides:* Pt. Ardel, Port Vila, Efate, on brown algae, low tide (2). Hotel Tanna, Tanna Is., on algae, low tide (2).

DISTRIBUTION AND HABITAT. New Hebrides, on algae and dead coral at low water (fig. 19).

REMARKS. This species is similar to the banded form of *E. (E.) ardeae* nov. in general appearance but is broader, with a more distinct, white basal band and a wider white band on the penultimate and body whorls, leaving only a relatively narrow brown band abapical and another adapical to the suture. The central white band is made up of close-set, dense white blotches usually alternating with narrow, translucent, colourless patches, whereas this band (when present) is uniformly dense-white in *E. (E.) ardeae*. The outer lip is more strongly prosocline in *E. (E.) colorata* than in *E. (E.) ardeae* and it lacks the vertical white marking which is often present abaperturally to the outer lip in *E. (E.) ardeae*. The radula of *E. (E.) ardeae* is similar to that of *E. (E.) colorata* only in the characters of the lateral teeth. The lack of denticles on the inner face of the central teeth of *E. (E.) colorata* is atypical for the subgenus and in marked contrast to the structure of the central teeth in *E. (E.) ardeae*.

*E. (E.) colorata* is probably more closely related to *E. (E.) pulicaria* (Fischer) but differs sufficiently in its radular features to allow full specific differentiation. It can be distinguished from both subspecies of *E. (E.) pulicaria* by its distinctly banded shell. The apertural details, general appearance and basic colour pattern are closer to those of *E. (E.) pulicaria pulicaria* than to *E. (E.) pulicaria pacifica*.

### **Eatonina (Eatonina) condita** sp. nov.

Figs 2e; 9a-f

Derivation of name: *conditus* (Latin) = secret, hidden.

DESCRIPTION. *Shell.* Minute, conical, opaque to subopaque, smooth, nonumbilicate, dark brown. Protoconch of 1½ smooth whorls, teleoconch of 3 very weakly convex whorls; surface smooth except for very indistinct growth lines. Periphery weakly subangled to rounded. Aperture subcircular, inner lip narrow, with almost straight edge, abapical portion separated a little from base. Outer lip orthocline to slightly prosocline. Suture sharply bent just abaperturally to outer lip. Umbilical chink small, no umbilicus. Colour uniformly dark brown, sometimes with a reddish or orange tinge. Inner lip of aperture red-brown, darker than rest of shell; yellowish or yellowish-brown immediately abaperturally to edge of outer lip.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.30 mm | 0.80 mm |
| Figured specimens | | |
| Paratypes (SEM stub no. 425) | 1.31 mm | 0.83 mm |
| (SEM stub no. 541) | 1.28 mm | 0.86 mm |
| (SEM stub no. 542) | 1.30 mm | 0.87 mm |

*Operculum.* Typical of genus (fig. 9b).

*Radula.* Central tooth with cutting edge reduced to an almost straight line with only 2 very weak denticles representing cusps and a weak median denticle on upper edge; lateral folds well developed. Lateral teeth with upper edge straight, upper inner edge swung sharply downwards at 45° to upper edge; innermost 2 cusps broad, rather blunt, outer 2 cusps small, sharp. Inner lateral teeth with 3 cusps, innermost long, middle very long, outer short. Outer marginal teeth with 4 sharp cusps, the third the longest (figs 9e, f).

Opercula and radulae examined from type locality and the localities from which additional paratypes were obtained (SEM stub nos 425, 531, 541, 542) and Normanville, S.A. (SEM stub no. 438).

TYPES. Holotype (C. 107151), Paratypes 4 (C. 107152); 18/9w (C. 107153), 11 (C. 107154), 21 (C. 107155) AM; 2 (E10104) TM; 2 (F 30096) NMV; 2 (D. 16107) SAM; 3 shells, 2 opercula and 4 radulae (SEM stub nos 425, 531, 541, 542).

TYPE LOCALITY. Goat Is., near Ulverstone, N. Tasm., stone washings (C. 107151, C. 107152), on coralline algae (C. 107153), on brown algae (C. 107154), 18 Mar. 1975, coll. W. F. Ponder and R. Kershaw.

LOCALITY FOR ADDITIONAL PARATYPES. Wedge Bay, S. Tasm., 13 m, J. Voorwinde Coll. (C. 107155).

ADDITIONAL MATERIAL EXAMINED *Tasm.:* West Head, Green Beach, under stones, rocky shore, low tide (2). Browns River, S. of Hobart (3). Fluted Cape, Bruny Is., 13-15 m, on algae at base of cliff (4). *Vic.:* S.E. side of Gabo Is., 28 m, on algae in sponge bed (1). S.S.E. of Gabo Is., 28 m, on red algae (2). Bastion Pt., S. tip of Mallacoota, intertidal (1). *S.A.:* ca. 3 km S. of Normanville, rocky platform (5). Hardwicke Bay (1). Streaky Bay, exposed coast, S. of township, on algae (9).

DISTRIBUTION AND HABITAT. Tasmania, Victoria and South Australia, on algae and under stones in the lower littoral and sublittoral (fig. 21).

REMARKS. This species is very similar in shell characters to *E. (Coriandria) fulvicolumella* nov. which is contrasted with *E. (E.) condita* where *E. (C.) fulvicolumella* is introduced below. The shell of *E. (E.) rubrilabiata* nov. is very similar in general appearance and in the aperture having a dark inner lip, but it is more ovate in shape. The shell of *E. (E.) sanguinolenta* nov. is also very similar to *E. (E.) condita* in general appearance but is slightly larger, has a rather glossy surface and is usually slightly more ovate in outline. *E. (E.) sanguinolenta* is also more red than brown and tends to be more translucent. The distribution of *E. (E.) hutchingsae* nov. overlaps that of *E. (E.) condita* but can be readily distinguished by its ovate shell, strongly convex whorls and relatively pale orange-brown colour.

Despite the similarity in shell characters the radulae serve to readily separate all of the above species (compare figs 6g; 9e, f; 9i, j; 10c, f; 11c, d).

### **Eatonina (Eatonina) hedleyi** sp. nov.

Figs 3e; 10j-l

DESCRIPTION. *Shell.* Minute, turbinate, with convex whorls, umbilicate, uniformly brown. Protoconch of 1½ smooth, shining whorls; teleoconch of up to 2 strongly convex whorls, smooth except for rather distinct growth lines, these particularly conspicuous within umbilical area. Aperture broadly oval, inner lip with weakly concave edge, connected to parietal wall for about ⅓ of its length, remainder tree, thin, lamella-like;

outer lip simple, very slightly prosocline. Umbilicus broad externally, perforation narrow. Colour dark orange-brown, outer lip yellowish-brown; inner lip slightly darker than rest of shell.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 0.77 mm | 0.66 mm |
| Figured specimen | | |
| Paratype (SEM stub no. 503) | 0.70 mm | 0.66 mm |

*Operculum*. Typical (fig. 10k).

*Radula*. Typical of subgenus; very similar to that of *E. (E.) capricornea* except outer marginal teeth relatively smaller, about ⅓ length of lateral teeth, compared with about ½ length of lateral teeth in *E. (E.) capricornea*. Both species peculiar in having inner edge of basal part of inner lateral teeth serrated (fig. 10l).

Opercula and radulae examined from type locality (SEM stub nos 487, 503).

TYPES. Holotype (C. 106267) and 10 paratypes (C. 106268), AM; 2 shells, 3 opercula and 2 radulae (SEM stub nos 487, 503).

TYPE LOCALITY. Off Sow and Pigs Reef, Sydney, N.S.W., shell sand, 5 m, 30 Sept. 1976, coll. A. Jones and J. Lowry.

DISTRIBUTION AND HABITAT. Known only from the type locality in Sydney Harbour, N.S.W., where it was obtained living in shelly sand in the sublittoral (fig. 19).

REMARKS. The radular features of this species show that it is related to *E. (E.) capricornea* but the shell of *E. (E.) hedleyi* differs in being much smaller and having a relatively shorter spire, a wider umbilicus and more convex whorls than *E. (E.) capricornea*. The serrated inner edge of the inner marginal teeth has not been observed in any species other than *E. (E.) hedleyi* and *E. (E.) capricornea*.

This species is named in recognition of Charles Hedley (1862-1926) who contributed so much to the knowledge of Australian Mollusca.

### **Eatonina (Eatonina) heliciformis** sp. nov.

Figs 3d; 10g-i

Derivation of name: shell shaped like *Helix*.

DESCRIPTION. *Shell*. Minute, depressed, heliciform, smooth, subopaque to translucent, umbilicate, with dark spiral bands and white blotches. Protoconch of about 1½ whorls; teleoconch of about 2 convex, smooth whorls. Aperture subcircular, weakly angled adapically, inner lip thin, narrow, separated from base at umbilical area; edge of outer lip prosocline. Umbilicus broad externally, perforation minute. Colour of body whorl pale yellowish-white to yellowish, with 4 narrow, dark red-brown bands on body whorl and a fifth, usually broad, band around umbilicus. Two rows of rather irregular dense white blotches on body whorl, one just abapical to suture, extending on to last half of penultimate whorl, and the other on periphery, these two sometimes coalescing on last ¼ of body whorl. Inner lip dark red-brown, outer lip yellowish-white; spire and protoconch dark red-brown, body whorl coloration developing on last half of penultimate whorl.

| Dimensions | Length | Diameter |
|---|---|---|
| Holotype | 0.95 mm | 0.82 mm |
| Paratype | 0.96 mm | 0.80 mm |
| Figured specimen<br>Paratype (SEM stub no. 461) | 0.96 mm | 0.76 mm |

*Operculum*. Typical (fig. 10h).

*Radula*. Typical of subgenus; central teeth with a pair of long denticles on inner face, a small, low protuberance on upper edge and broad, curved lateral folds. Lateral teeth with low swelling on upper inner edge; 5 comb-like cusps on inner side of large, blunt, main cusp and 3-4 small cusps and 0-2 denticles on outer side. Inner marginal teeth with 3-4 cusps, first and second long, second largest. Outer marginal teeth with 3-4 short cusps (fig. 10i).

Opercula and radulae examined from type locality (SEM stub no. 461) and from Noumea, New Caledonia (SEM stub no. 216).

TYPES. Holotype (C.106172) and 5/3w paratypes (C.106173), AM; 1 shell, 1 operculum and 1 radula (SEM stub no. 461).

TYPE LOCALITY. Pt. Ardel, Port Vila, Efate, New Hebrides, on brown algae, low tide, 16 Jan. 1967, coll. W. F. Ponder.

ADDITIONAL MATERIAL EXAMINED. *New Hebrides:* Port Vila, Efate, on algae, sheltered reef (4). Pt. Ardel, Port Vila, Efate, coral block washings, low tide (2). *New Caledonia:* Baie de Radio Etat, Magenta, semi-sheltered, rock, algae and coral (4).

DISTRIBUTION AND HABITAT. New Hebrides and New Caledonia in the lower littoral on algae, dead coral and rocks (fig. 20).

REMARKS. The depressed, heliciform shell with its distinctive colour pattern and prominent umbilicus readily distinguish this species from all other named Australian and tropical Pacific species. *Eatonina (Eatonina) maculosa* Ponder from northern New Zealand is similar in shape and also has 2 rows of dense-white spots but lacks any colour bands. An unnamed species known only from two subadults collected at Heron Is., Queensland is very similar to *E. (E.) heliciformis* but there is insufficient material to describe it adequately.

### **Eatonina (Eatonina) hutchingsae** sp. nov.

Figs 2f; 10a-f

DESCRIPTION. *Shell*. Minute, ovate-conical, solid, smooth, opaque, orange-brown, nonumbilicate. Protoconch of 1½ smooth whorls; teleoconch of 2½ convex whorls, smooth except for fine growth lines and very inconspicuous spiral scratches. Aperture subcircular, sometimes slightly separated from body whorl; outer lip thin, slightly prosocline; inner lip with weakly concave edge, rather narrow. Colour orange-brown, fading to yellow at the outer lip; inner lip and columella darker brown than rest of shell.

| Dimensions | Length | Diameter |
|---|---|---|
| Holotype | 1.24 mm | 0.83 mm |
| Paratype | 1.23 mm | 0.80 mm |

Figured specimens

| | | |
|---|---|---|
| Solitary Is., N.S.W. (SEM stub no. 437) | 1.14 mm | 0.82 mm |
| Gabo Is., Vic. (SEM stub no. 467) | 1.28 mm | 0.87 mm |

*Operculum.* Typical (fig. 10e).

*Radula.* Typical of subgenus; central tooth with 2 pairs of denticles on inner face, a low, knob-like swelling on upper edge and prominent lateral folds. Lateral teeth with 4-6 comb-like cusps on inner side of long, rather sharp main cusp; 3-4 small cusps, and usually a few very small accessory denticles, on outer side of main cusp. Inner marginal teeth with 4-5 sharp cusps, the second from inside longest. Outer marginal teeth with 7-8 cusps, 3(?)-4 on outer end, 2-3 shorter cusps on lower forward edge (figs 10b, c, f).

Opercula and radulae examined from type locality (SEM stub no. 457), Solitary Is., N.S.W. (SEM stub no. 437) and Gabo Is., Vic. (SEM stub nos 135, 467).

TYPES. Holotype (C. 106175), 5 paratypes (C. 106176), 7/5w paratypes (C. 106174), 3 paratypes (C. 106177), AM; 2 paratypes (MO 6314), QM; 1 paratype (E 9815), TM; 1 paratype (F 30044), NMV; 1 shell, 1 operculum and 1 radula (SEM stub no. 457).

TYPE LOCALITY. S. side of Caloundra Head, Caloundra, Qld, on coralline algae (C. 106176), on algae (C. 106174) and under rocks (C. 106177), on exposed rock platform, from tide pool, 20 Oct. 1976, coll. I. Loch and B. Duckworth.

ADDITIONAL MATERIAL EXAMINED. *Qld:* Noosa Heads (1). Caloundra Beach (3). *N.S.W.:* Ballina, on algae (1). S.W. of Solitary Is., 15 m (3). Fingal Bay, Port Stephens (9). Pittwater, Broken Bay, dredged (1). Chinamans Beach, Middle Harbour, Sydney, 5 m (13). Sow and Pigs Reef, Sydney, 9 m (9); 13-16 m (6). Parsley Bay, Sydney, 9 m, on red algae (1). Green Cape, Disaster Bay, 15 m (4). S. end of Green Cape, Disaster Bay, 2-4 m, on algae (1). *Tasm.:* Pirates Bay, Eaglehawk Neck (5); under stones (4). Derwent Estuary (1). *Vic.:* E. of Monument Bay, Gabo Is., 7-10 m (2). Below lighthouse, E.S.E. side of Gabo Is., 15-18 m on algae and detritus (10). S.S.E. side of Gabo Is., 28 m, red algae (1); 28 m, algae in sponge bed (3). Pt. Hicks, Cape Everard, 18 m (5).

DISTRIBUTION AND HABITAT. Noosa Heads, southern Queensland to eastern-most Victoria and eastern Tasmania on algae and debris in the lower littoral and sublittoral (fig. 20).

REMARKS. This species is similar in shape and colour to *Eatonina atomaria* (Powell) from New Zealand but differs in having less convex whorls and being a little more conical in shape and nonumbilicate. *Eatonina shirleyae* nov. is also similar to *E. (E.) hutchingsae* but is darker in colour, has a more strongly retracted outer lip, more conspicuous spiral striae and less convex whorls. Another somewhat similar species, *E. rubrilabiata* nov. is contrasted with *E. hutchingsae* below.

This species has been named for Dr Patricia Hutchings who has provided us with numerous sublittoral samples containing micro-molluscs.

### **Eatonina (Eatonina) lactea** sp. nov.

Figs 3f; 8k-o

Derivation of name: *lacteus* (Latin) = milky white.

DESCRIPTION. *Shell.* Minute, narrowly conic, solid, smooth, nonumbilicate, translucent to subopaque white to reddish-brown, with 2 rows of large opaque white spots on body whorl. Protoconch of 1½ whorls, teleoconch of 3½ slightly convex whorls, smooth except for growth lines. Aperture circular to sub-circular, inner lip moderately wide, its edge convex in mature examples, adapical portion separated from base as a thin lamella; outer lip slightly prosocline, a weak varix usually present. Suture bent sharply abapically just abaperturally to edge of outer lip. Umbilical chink very small or absent, no umbilicus. Colour translucent white with very broad axial patches of dense white on spire whorls which reduce translucent parts of shell to narrow, broken, often zig-zag axial streaks of the basic shell colour. White patches broken into 2 series on body whorl with a series of large, squarish blotches on adapical part of whorl terminating just above periphery, these separated from, or narrowly connected to, a row of rounded blotches on adapical half of base sometimes about twice as numerous as the larger series of blotches. Remainder of base and aperture translucent white to reddish-brown.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.54 mm | 0.84 mm |
| Paratypes | 1.40 mm | 0.76 mm |
| Figured specimen | | |
| Paratypes (SEM stub no. 527) | 1.52 mm | 0.80 mm |

*Operculum.* Typical of genus (figs 8l, m).

*Radula.* Central tooth much wider than deep, with weakly convex "cutting edge", a weak median denticle on concave upper edge; lateral folds well developed; inner face much reduced, denticles probably absent. Lateral teeth with upper edge convex, with 7-9 cusps, innermost bifid, the next larger and blunt, the following cusps sharp and decreasing in size outwards. Inner marginal teeth with long, sharp cusps, innermost (2?) slightly shorter than the next, which is followed by 1-2 short cusps and then another long cusp and 2-4 short cusps. Outer marginal teeth with 3 sharp inner cusps followed by a larger sharp cusp and 1-2 short cusps (figs 8n, o).

Opercula and radulae examined from type locality (SEM stub no. 527) and W. Rarotonga, S. Cook Ids (SEM stub no. 493).

TYPES. Holotype ANSP (278391) and 11 paratypes ANSP (344916); 12 paratypes ANSP (278043); 5 paratypes AM (C. 108289); 1 shell, 1 operculum and 2 radulae (SEM stub no. 527).

TYPE LOCALITY. 1.6 km S.W. of Aitutaki, N. Cook Ids, 1-6 m, on coral, 19 Feb. 1962, coll. R. W. Forster & R. Ostheimer, holotype and 11 paratypes, ANSP (278391, 344916).

LOCALITY FOR ADDITIONAL PARATYPES. E. side Akitua, N.E. Aitutaki, N. Cook Ids, 0-1 m, rocks, sand, sea grass and coral, Feb. 1962, coll. D Ashton, R. W. Forster & R. Ostheimer (ANSP 278043); (AM C. 108289).

ADDITIONAL MATERIAL EXAMINED. *S. Cook Ids:* 1.6 km N. of Arorangi Village, W. Rarotonga, 0-1.5 m, amongst coral, sand and rocks (14) ANSP (279105), SEM stub no. 493. 4 km N. of Matavera, N.E. Rarotonga (4) ANSP (278830). Avarua Passage, N. Rarotonga, 12-14 m, sand pebbles and stones (16) ANSP (278581).

DISTRIBUTION AND HABITAT. Cook Ids, living in the lower littoral and sublittoral (fig. 18).

REMARKS. The ground colour varies from translucent to subopaque white through yellow to red-brown. Two series (ANSP 279105, 278581), show a range of colour varying from pale yellow to pale or dark brown, another lot (ANSP 278830) are all red-brown, and the type lot and one other (ANSP 278043) are all white to pale yellow. There is also fairly considerable variation in size. This species is very similar to *E. (E.) pulicaria pacifica* nov. in most features but can be distinguished by its more elongate form and the details of the colour pattern as well as by the different radula. *E. (E.) lunata* (Laseron) is also similar but is larger, has a more variable and slightly different colour pattern and the radula is also distinct.

The peculiar central tooth of this species may have been derived from a tooth similar to that of *E. (E.) pulicaria* (Fischer) by the lateral folds meeting dorsally. The face of the tooth has shortened and is swung backwards and upwards and, presumably because the denticles in this position would be functionless, they have apparently been lost (no photographs are available that show the face sufficiently well to determine the total absence of any denticles). The lateral teeth lack a distinct bulge on their upper edges and their cusps are, probably as a result, more uniform in size than those seen in most species of *Eatonina* s.s. The radula of *E. (E.) lactea,* although not typical of *Eatonina* s.s., is, as shown above, capable of being derived from a radula more typical of the subgenus and, because the shell also bears a close resemblance of the shell to *E. (E.) pulicaria,* this species is included in *Eatonina* s.s.

### **Eatonina (Eatonina) lunata** (Laseron, 1956)

Figs 3g; 5g, h; 8a-e

*Estea lunata* Laseron, 1956: 441, fig. 147.

DESCRIPTION. *Shell.* Minute, ovate-conical, solid, smooth, subopaque to opaque, nonumbilicate, yellowish-white to dark brown, with white blotches. Protoconch of 1½ smooth whorls; teleoconch of up to 4 weakly convex whorls, smooth except for inconspicuous growth lines and spiral striae. Aperture subcircular to circular, constricted adapically when mature, peristome thin, outer lip sharp, thickened abaperturally in adapical portion to form a weak varix-like swelling. Abapical portion of inner lip separated from base as a thin lamella; outer lip orthocline. Suture swings sharply abapically just adaperturally to aperture. Colour yellowish-white to dark orange-brown, patterned with dense milky-white markings. Pattern in form of blotches, spots, zig-zag lines, or a broad band on adapical half of spire whorls; blotches sometimes merge to give an almost uniform dense-white shell colour; often a row of small white spots on periphery. Base usually with zig-zag markings but sometimes uniform white, spotted, or without any white markings.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.86 mm | 1.10 mm |
| Paratype | 1.93 mm | 1.10 mm |
| Figured specimens | | |
| Noumea, New Caledonia (SEM stub no. 140) | 1.48 mm | 0.88 mm |
| Lizard Is., Qld (SEM stub No. 157) | 2.20 mm | 1.18 mm |

*Operculum.* Typical (fig. 8d).

*Radula.* Typical of subgenus; central tooth with a pair of weak denticles on inner face; upper edge horizontal to slightly concave, weakly thickened, with a very low median swelling present when tilted forward; lateral folds broad, curved. Lateral teeth with prominent swelling on upper inner edge; 2-3 small cusps on inner side of large, rather blunt, main cusp and 6-9 cusps on outer side. Inner marginal teeth with 5-8 cusps spread along most of forward edge, innermost two cusps longer than rest, second cusp longest (fig. 8e).

Opercula and radulae examined from Lizard Is., Qld (SEM stub no. 157) and Noumea, New Caledonia (SEM stub no. 140).

*Head-foot.* Typical of family; tentacles rather long, lash rapidly up and down as animal moves, with eyes in small bulges at their outer bases. A small triangular dense-white patch immediately behind eyes. Snout small, bilobed, pale yellow to orange, rest of head usually colourless or yellowish, sometimes orange. Buccal mass bright orange. Foot long, bluntly rounded in front, sharply rounded posteriorly, propodium small, its edge usually not extending to margin of foot, posterior mucous slit along posterior half of foot. Dorsal foot reddish-orange posteriorly, yellowish with red margins anteriorly. Opercular lobe with small, dense-white patch on either side (specimens examined from Lizard Is., Qld).

TYPES. Holotype (C. 105673) and 44 paratypes (C. 106178), AM.

TYPE LOCALITY. Bowen, Qld, on algae, coll. J. Laseron.

ADDITIONAL MATERIAL EXAMINED. *Papua New Guinea:* Amazon Bay, Milne Bay Province, 13 m, on algae (1). *Coral Sea:* Herald Cay, 5-7 m (33). *New Caledonia:* Recif Bay, Poum, 1-4 m, algae on dead coral on sandy mud (2). Bay of Magenta, Noumea, 0-1 m, under rocks (1). W. side of Ile Signal, Noumea, 0-2 m, on algae on sand and coral bottom (42). *Qld:* S. end of Casuarina Beach, Lizard Is., 1-2 m (17). Between Lizard and Palfrey Is., Lizard Is., 1.5 m, on coralline algae, on sandy bottom with coral outcrops (40/12w). S.W. of Euston Reef, off Cairns, 21 m (9). King Reef, off Kurrimine Beach, S. of Innisfail, on algae (1). Headland between Kings and Queens Beaches, Port Denison, Bowen, 1 m, on algae (43). Heron Is., 11 m (1); 91 m (1).

DISTRIBUTION AND HABITAT. Papua New Guinea, New Caledonia, Coral Sea and the Great Barrier Reef, Queensland, on algae and debris, lower littoral and sublittoral (fig. 20).

REMARKS. The shell of this species differs from the other Australian species of the genus in having a distinctive colour pattern, an elongate conical form and nearly circular to circular, somewhat constricted, aperture. *Eatonina (E.) pulicaria* (Fischer) and its subspecies *pacifica* nov. have a somewhat similar colour pattern but are much smaller.

The type series of this species represents a population with shells slightly smaller than the normal form of the species. This species probably has a wider range in the S.W. Pacific than is known at present.

### Eatonina (Eatonina) pulicaria pulicaria

(Fischer (in Folin & Périer, 1873))

Figs 3b; 7f-k

*Cingula pulicaria* Fischer (in Folin & Périer), 1873:207, pl. 9, fig. 4.

DESCRIPTION. *Shell.* Minute, rather narrowly ovate-conical, solid, opaque to subopaque, smooth, nonumbilicate, white with rectangular markings, base and inner lip dark brown. Protoconch of 1½ whorls; teleoconch of 2½ lightly convex whorls; smooth except for growth lines. Aperture subcircular, slightly angled in adapical corner; inner lip narrow, edge nearly straight, abapical portion hardly separated from base; outer lip orthocline, simple. Suture bent abapically just abaperturally to edge of outer lip. Umbilical chink distinct, no umbilicus. Colour milky white, abapical half of base and inner lip dark brown; vertically elongated rectangular patches on spire whorls and body whorl translucent yellow-brown with dark brown spots in their adapical and abapical extremities, the abapical row of spots occasionally connected to form a spiral band; abapical row of spots clearly visible within aperture.

Dimensions

| | Length | Diameter |
|---|---|---|
| "Type" (from original description) | 1 mm | 0.33 mm |
| Paratype (?) (from deFolin Coll.) | 1.13 mm | 0.78 mm |
| Figured specimens | | |
| Mauritius (SEM stub no. 306) | 1.08 mm | 0.68 mm |
| Mauritius (SEM stub no. 494) | 1.16 mm | 0.70 mm |

*Operculum.* Typical (figs 7g, k).

*Radula.* Typical of subgenus; central tooth with a pair of weak denticles on inner face; a small median cusp on upper edge and strongly curved lateral folds. Lateral teeth with low swelling on upper inner edge; 1-2 weak denticles on inner side of massive, almost square, main cusp and 3-6 small cusps on outer side; straight edge of main cusp very weakly serrated. Inner marginal teeth with 3 sharp, rather long, cusps, middle one longest, up to 5 additional small cusps sometimes present; 2 supporting structures present, outermost larger. Outer marginal teeth with 4-5 small cusps (fig. 7j).

The radula of a specimen of this species from Arsenal Bay, Mauritius (SEM stub no. 306) agrees with that of the other 2 lots of Mauritius material examined except that the inner marginal teeth have 3-5 cusps on the outer side of the median cusp, instead of 1-2 (fig. 7h).

Opercula and radulae examined from Tombeau Bay and Point Fayette, Mauritius (SEM stub nos 494, 495) and Mauritius (SEM stub no. 462).

TYPES. deFolin material in BMNH and AM (C. 106213) (paratypes?).

TYPE LOCALITY. Mauritius, coll. M. Dupont.

ADDITIONAL MATERIAL EXAMINED. *Mauritius:* No other data (Muséum National d'Histoire Naturelle, Paris). *W. Mauritius:* Flicq-en-Flacq, Arsenal Bay (many) (NMNH 716525 & 716538); weed rock and coral, 9 m (4) (ANSP 273191). Pt. Pimente, N. side Arsenal Bay, rocks, sand and coral, 0-1 m (11) (ANSP 273068). N.W. tip, Arsenal Bay (15) (NMNH 716576). 2.4 km N.W. of Black River, 14 m, sand, shell and some weed (3) (ANSP 273342). S. side of Tombeau Bay, weed, sand and rocks, 0-5 m (many) (ANSP 273271) (SEM stub no. 494). *E. Mauritius:* Pt. Fayette, weed, sand, rock and coral, 0-2.5 m (many) (ANSP 273727) (SEM stub no. 495). Pt. des Puits, near Centre de Flacq, on algae (many/23w). *S.E. Mauritius:* Le Chaland, 4 km S. of Mahebourg, on algae, semi-exposed rocks, low tide (many).

DISTIRIBUTION AND HABITAT. Mauritius, Indian Ocean, on algae and debris in the lower littoral and in the sublittoral (fig. 18).

REMARKS. This subspecies is compared with *E. (E.) pulicaria pacifica* nov. below.

### **Eatonina (Eatonina) pulicaria pacifica** subsp. nov.

Figs 3c; 7l-n

Derivation of name: from Pacific Ocean.

DESCRIPTION. *Shell.* Minute, rather broadly ovate-conical, solid, opaque to subopaque, smooth, nonumbilicate, white with small dark brown spots; inner lip and base brown. Protoconch of 1½ whorls; teleoconch of 2¼ lightly convex whorls; smooth except for growth lines. Aperture subcircular, slightly angled in adapical corner, inner lip narrow, edge nearly straight, abapical portion separated from base as a low lamella; outer lip orthocline, simple. Suture bent abapically just abaperturally to edge of outer lip. Umbilical chink distinct, but no umbilicus. Colour dense white, base pale to dark brown, usually with a row of small peripheral brown spots and sometimes a much weaker median row of spots abapical to suture, both rows, when present, visible on spire whorls as well as on body whorl; peripheral row of spots sometimes connected by narrow flames to abapical half of base; inner lip with pale edge, dark brown within aperture.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.20 mm | 0.82 mm |
| Figured specimen<br>Paratype (SEM stub no. 107) | 1.30 mm | 0.87 mm |

*Operculum.* Typical (fig. 7m).

*Radula.* Typical of subgenus; central tooth with a pair of rather small denticles on inner face; a small, knob-like denticle on upper edge and prominent, curved lateral folds. Lateral teeth with prominent swelling on upper inner edge, a rather large cusp inside and outside massive triangular main cusp, 1-2 small cusps on median part of cutting edge; supporting structure weakly bifid or single. Inner marginal teeth with 4 short cusps (fig. 7n).

Opercula and radulae examined from type locality (SEM stub no. 107).

TYPES. Holotype (C. 106179) and 37 paratypes (C. 106180), and many paratypes/many wet (C. 106181, C. 106182) AM; 4 paratypes (345990) ANSP; 2 shells, 1 operculum and 2 radulae (SEM stub no. 107).

TYPE LOCALITY. Pt. Ardel, Port Vila, Efate, New Hebrides, on brown algae (C. 106180); on algae (C. 106182); coral block washings (C. 106181), all low tide, Jan 1967, coll. W. F. Ponder.

DISTRIBUTION AND HABITAT. New Hebrides, on algae and rubble in the lower littoral (fig. 18).

REMARKS. The shell of the new subspecies differs from *Eatonina pulicaria pulicaria* in being a little broader, in having a more distinct umbilical chink, 1-2 rows of brown spots on the body whorl instead of a single row of brown rectangular markings and the abapical portion of the inner lip separated from the base to a greater extent. The radula shows a number of minor distinctions, the most notable being the differences in the lateral teeth, and in particular in the shape of the median cusp which is pointed in *E. (E.) pulicaria pacifica* and has a broad, straight edge in *E. (E.) pulicaria pulicaria.*

It is not known whether the disjunct distribution of this species is the result of poor collecting in intervening areas or if the two subspecies are relict populations of a previously much more widely distributed species.

### **Eatonina (Eatonina) rubrilabiata** sp. nov.

Figs 2g; 6e-g

Derivation of name: *ruber* (Latin) = red, *labia* (Latin) = lip.

DESCRIPTION. *Shell.* Minute, ovate-conical, rather solid, surface smooth and shining, slightly translucent, dark orange brown. Protoconch of 1½ whorls; teleoconch of 2½-2¾ lightly convex to moderately convex whorls, smooth except for fine growth lines. Aperture subcircular, inner lip narrow, its edge slightly concave, somewhat thickened and raised from parietal wall in adapical portion and well separated from the base abapically; outer lip simple, orthocline; suture bent abapically just abaperturally to outer lip. Umbilical chink distinct, umbilicus closed or very narrowly open. Colour dark orange brown, umbilical area and a narrow line just abapical to suture darker than rest of shell; outer lip and a narrow zone adapertural to it yellow; inner lip very dark reddish-purple to dark orange-brown.

| Dimensions | Length | Diameter |
|---|---|---|
| Holotype | 1.33 mm | 0.90 mm |
| Paratype | 1.26 mm | 0.87 mm |
| Figured specimen<br>Paratype (SEM stub no. 460) | 1.28 mm | 0.83 mm |

*Operculum.* Typical, internal ridge very weak to absent (fig. 6f).

*Radula.* Typical of subgenus; central teeth with 2 pairs of very prominent denticles on inner face, cutting edge weakly convex, a very small denticle at either end of cutting edge and one in middle. Lateral teeth with very prominent, knob-like swelling on upper inner edge; 3 small cusps on inner side of sharp, prominent main cusp and 3-4 small cusps on outer side. Inner marginal teeth with 3 long, sharp cusps, and sometimes 2 additional small cusps on outer side of third cusp; 2 supporting structures present, outer one longest. Outer marginal teeth rather large, with 3 sharp cusps (fig. 6g).

Opercula and radulae examined from type locality (SEM stub nos 330, 459 & 460).

TYPES. Holotype (C. 106184) and 16/10w paratypes (C. 106185), AM; 3 paratypes (F. 30045), NMV; 3 shells, 6 opercula and 5 radulae (SEM stubs nos 330, 459 & 460).

TYPE LOCALITY. On seaward side of the long rocky point at Batehaven, Batemans Bay, N.S.W. on *Champia*, medium exposure, 6 Jan. 1970, coll. W. F. Ponder and P. H. Colman.

ADDITIONAL MATERIAL EXAMINED. *N.S.W.*: Fingal Bay, Port Stephens (11). Pittwater, Broken Bay, dredged (1). Off Patonga Beach, Broken Bay, dredged (5). Collaroy Beach, near Sydney (3). Ocean beach, Manly (14). North Harbour, Sydney dredged (2). Off Chinamans Beach, North Harbour, Sydney, 5m (35). Off Sow and Pigs Reef, Sydney (6); 9m (14). 2.6km E. of Maroubra Beach, Sydney, 58 m (1). Ocean beach, Kurnell, Botany Bay (1). Ulladulla (5). Wimbie Beach, Batemans Bay, under stones, rocky, exposed shore (1). Batemans Bay (7). Merimbula Jetty, Merimbula, stone washings, exposed shore (3). Green Cape, Disaster Bay side, 15 m (2). N. side Black Head, Nadgee, coralline algae on exposed rocks (2).

DISTRIBUTION AND HABITAT. New South Wales, at least as far north as Port Stephens and to the southernmost part of the state, in the lower littoral and the sublittoral on algae and under rocks (fig. 20).

REMARKS. This species has a similar shell to *Eatonina (E.) hutchingsae* nov., *Eatonina (E.) sanguinolenta* nov., and *Eatonina (Coriandria) rubicunda* nov. It is contrasted with the latter two species where they are introduced. It differs from *Eatonina (E.) hutchingsae* with which it is sympatric, in being darker in colour, more conical in outline and in having a relatively smaller body whorl. The outer lip is orthocline, not prosocline as in *Eatonina (E.) hutchingsae*, and the adapical portion of the inner lip is raised from the parietal wall and is very dark in colour, whereas it is flush with the parietal wall and relatively paler in *E. (E.) hutchingsae*. The abapical portion of the inner lip is well separated from the base in *E. (E.) rubrilabiata* but not in *E. (E.) hutchingsae*. The radulae of the two species differ in the details of the cusp patterns of all the teeth. Beach shells frequently appear to have the entire peristome coloured red-brown, but this is generally not apparent in fresh material.

### **Eatonina (Eatonina) sanguinolenta** sp. nov.

Figs 2d; 9g-j

Derivation of name: *sanguinolentus* (Latin) – stained with blood; refers to the colour of the shell.

DESCRIPTION. *Shell.* Minute, ovate-conical, subopaque to translucent, smooth, shining nonumbilicate, dark red-brown. Protoconch of about 1½ smooth whorls; teleoconch of 2¾-3 weakly convex whorls; surface smooth except for weak growth lines and extremely fine spiral scratches. Periphery evenly convex. Aperture subcircular, inner lip narrow, with edge almost straight, abapical portion separated a little from base. Outer lip orthocline to slightly prosocline. Suture sharply bent abapically just abaperturally to outer lip. Umbilical chink small, no umbilicus present. Colour dark red-brown, inner lip darker wine-red to dark purplish-red; outer lip yellowish-brown; sutures often false margined and appear darker in colour than rest of spire, umbilical area usually very dark red-brown.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.46 mm | 0.92 mm |
| Paratype | 1.43 mm | 0.93 mm |
| Figured specimen | | |
| Paratype (SEM stub no. 329) | 1.42 mm | 0.90 mm |

*Operculum.* Typical of genus (fig. 9h).

*Radula.* Central tooth with upright denticle in middle of concave upper edge; face of tooth thickened, otherwise simple; lateral folds extending ventrally beyond reduced inner face of teeth. Lateral teeth with weak swelling on upper inner edge; 6-7 cusps, innermost cusp weakly denticulate in one specimen, second cusp long, remainder decrease in size toward outside of teeth. Inner marginal teeth with 4 cusps, middle 2 cusps very long. Outer marginal teeth rather long, with 3 long cusps and one short cusp (figs 9i-j).

Opercula and radulae examined from type locality (SEM stub nos 329, 532) and Elliston, S.A. (SEM stub no. 428).

TYPES. Holotype (C. 106202) and 20/10w paratypes (C. 106203), 22 paratypes (C. 106204), AM; 2 (E 9817), TM; 2 (F 30046), NMV; 2 (D 15982), SAM; 1 shell, 5 opercula and 3 radulae (SEM stub no. 329) and 2 radulae (SEM stub no. 532).

TYPE LOCALITY. Point Sinclair, S.A., on algae, 0-1 m, limestone reef (C. 106203); shell sand (C. 106204), 9 Feb. 1972, coll. W. F. and J. M. Ponder.

ADDITIONAL MATERIAL EXAMINED. *Tasm*: Wedge Bay, 13 m (6). *Vic*: Ocean side of Queenscliff, Port Phillip, green algae on rock platform (1). *S.A.*: 0.6 km off Middle Pt., near Cape Northumberland, 6 m, on algae (2). Tumby Bay (90). Elliston, 0-5 m on algae (4).

DISTRIBUTION AND HABITAT. Tasmania, Victoria and South Australia, on littoral and sublittoral algae (fig. 21).

REMARKS. Paratypes of *Estea erma* Cotton, 1944 (SAM) are this species but the marked holotype is a species of *Microfossa* (Rissoidae). The radula of this species is somewhat atypical of the subgenus *Eatonina* in that the lateral teeth only have a weak swelling on the upper inner edge and the cusps are rather equally developed. The swelling on the face of the central tooth superficially resembles, in some specimens, a single broad cusp. This thickened area appears to be bilobed in some specimens and may represent a fused pair of denticles. The shell of this species is distinguishable from that of most other Australian species in the subgenus by its glossy surface, red colour and the dark inner lip of the aperture. *E. (E.) rubrilabiata* nov. is very similar in shell features but has a slightly duller surface, has a less prominent umbilical chink and its thinner lip is more distinctly raised from the parietal wall. *Eatonina (C.) rubicunda* nov. and *E. (E.) condita* nov. are both similar in shell features to *E. (E.) sanguinolenta* and are contrasted in the remarks on those species.

### **Eatonina (Eatonina) shirleyae** sp. nov.

Figs 2i; 6h-j

DESCRIPTION. *Shell*. Minute, ovate-conical, solid, smooth, subopaque, dark orange-brown, nonumbilicate to very narrowly umbilicate. Protoconch of 1½ smooth whorls; teleoconch of 2½ weakly convex whorls; smooth except for weak spiral striae and axial growth lines. Aperture subcircular to subpyriform in juveniles, inner lip thin, narrow, with a weakly concave edge, outer lip sharp, moderately prosocline. Colour uniform dark orange-brown,inner lip slightly darker in some specimens.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.37 mm | 0.94 mm |
| Paratype | 1.33 mm | 0.90 mm |
| Figured specimen<br>Paratype (SEM stub no. 148) | 1.35 mm | 0.91 mm |

*Operculum*. Typical (fig. 6i).

*Radula*. Typical of subgenus; central tooth similar to those of *E. rubrilabiata* nov., having 2 pairs of large denticles on inner face, but with narrower cutting edge and lateral folds more pointed below. Lateral teeth with moderate swelling on upper inner edge; a rather large cusp on inside separated by 2 small cusps from a large rectangular cusp followed by a slightly longer triangular cusp and then one small cusp. Inner marginal teeth with 4 cusps: — 2 middle cusps large with rounded distal ends, third cusp longest. Outer marginal teeth with 3 moderate cusps; one very small cusp on outer side (fig. 6j).

Operculum and radula examined from type locality (SEM stub no. 148).

TYPES. Holotype (C. 106187) and 9 paratypes (C. 106188), AM; 2 paratypes (WAM 393-77), WAM; 1 shell, 2 opercula and 2 radulae (SEM stub no. 148).

TYPE LOCALITY. Mississippi Bay, 48 km E. of Esperance, S.W.A., on sheltered side of

W. head of bay, 0-2 m, on algae, 6 Feb. 1972, coll. W. F. Ponder.

ADDITIONAL MATERIAL EXAMINED. *S.A.*: W. side of Thevenard, near Ceduna, low tide, short algae on semi-sheltered rock platform (2).

DISTRIBUTION AND HABITAT. Known only from the type locality in south Western Australia and one locality in South Australia where it was obtained on algae at low tide (fig. 21).

REMARKS. This species is most readily distinguished by its uniform dark coloration and retracted (i.e. prosocline) outer lip. The shell surface is sculptured with fine spiral striae which, in contrast with most related species, are easily visible under high magnification with a stereo-microscope. The most similar Australian species is *Eatonina (E.) hutchingsae* but that species is paler, has a noticably dark inner lip and the outer lip is less noticeably retracted (i.e. prosocline). *E. (Coriandria) rubicunda* nov. has a somewhat similar shell and is contrasted under that species.

This species is named for Mrs. Shirley Slack-Smith of the Western Australian Museum as a token of appreciation for her help in many ways to us.

### **Eatonina (Eatonina) striata** sp. nov.

Figs 2h; 9k, l

Derivation of name: *striatus* (Latin) = furrowed, ridged.

DESCRIPTION. *Shell.* Minute, conical, rather solid, surface shining, base with distinct spiral grooves, nonumbilicate, orange-brown. Protoconch of 1½ smooth whorls; teleoconch of 2¼ lightly convex whorls, with faint to moderate spiral striae on spire, usually with a strong spiral cord immediately abapical to suture and fine but distinct spiral grooves on base and periphery, usually becoming indistinct adapical to periphery. Weak, sometimes fairly distinct, prosocline growth lines (sometimes weak riblets) on spire and body whorl; growth lines sometimes render sutural cord weakly and finely nodulous. Aperture almost circular, inner lip narrow, abapical portion only slightly separated from base; outer lip simple, curved markedly adaperturally in its adapical portion. Colour dark orange-brown, outer lip yellowish, inner lip slightly darker orange-brown than rest of shell.

Dimensions

|  | Length | Diameter |
|---|---|---|
| Holotype | 1.08 mm | 0.70 mm |
| Paratype | 1.03 mm | 0.72 mm |

*Operculum.* Typical (fig. 9k).

*Radula.* Typical of subgenus with the exception of the central tooth which is rather small, with lateral folds at about 45° to vertical axis, without any structures on face of tooth apart from a weak vertical ridge; upper edge strongly convex. Lateral teeth with weak swelling on upper inner edge; a massive, subtriangular main cusp with about 3 denticles on its inner side and 2 on its outer. Inner marginal teeth with 5 small, widely-spaced cusps and a single supporting structure. Outer marginal teeth with 3 cusps and 1-3 denticles (fig. 9l).

Operculum and radula examined from type locality (SEM stub no. 473).

TYPES. Holotype (C. 106189) and 4 paratypes (C. 106190), AM; 1 paratype (WAM 394-77), WAM; 1 operculum and 1 radula (SEM stub no. 473).

TYPE LOCALITY. W. side Carnac Is., off Fremantle, W.A., on algae, 4-8 m, 18 Dec. 1971, coll. W. F. and J. M. Ponder, B. R. Wilson and N. Coleman.

DISTRIBUTION AND HABITAT. Known only from the type locality in Western Australia where it lives on algae in the sublittoral (fig. 21).

REMARKS. This species is the only one of the subgenus with distinct spiral sculpture, a sutural cord and, in some specimens very weak axial riblets. No other species appears to be closely related and it should not be confused with any other. The unusual central teeth are somewhat similar to those of *E. (E.) colorata* nov. which also has the inner marginal teeth bearing widely spaced cusps. In other respects the radulae are generally similar, but differ in detail, and the shells are extremely dissimilar.

### Subgenus **Captitonia** nov.

Type species: *Eatonina (Captitonia) lirata* sp. nov.

Derivation of name: *captio* (Latin) = a cheat, deception; refers to the greatly different features of the shell compared with other species of *Eatonina*.

DIAGNOSIS. Shell conical, with strong spiral keels, nonumbilicate, aperture with slightly retracted outer lip, protoconch with single weak keel, otherwise smooth. Operculum and radula as for *Eatonina* s.s.

DISTRIBUTION. South Western Australia and possibly northern New Zealand.

REMARKS. This subgenus is based on a strongly keeled species which, on shell characters, is very readily distinguishable from *Eatonina*. The radula and operculum are, however, so similar to those of species of *Eatonina*, the shells of which in some instances develop weak spiral sculpture, that *Captitonia* is here regarded as being only subgenerically distinct.

Some rissoid and eatoniellid genera such as *Tropidorissoia* Tomlin & Shackleford, 1915, *Liratoniella* Ponder, 1965 and *Lironoba* Iredale, 1915, resemble *Captitonia* particularly in the sculptural characters of the shell. *Tropidorissoia* is based on a thick-shelled rissoid with a protoconch bearing several weak spiral ridges. The aperture has a thickened peristome and the type species (*taphrodes* Tomlin & Shackleford) is umbilicate. The microsculpture of the teleoconch of both species included in the genus (*taphrodes* and *varicifera* Smith) is of fine spiral ridges which are not present in *Captitonia*.

The radular and opercular features of *Tropidorissoia* are not known but it is considered to be likely that they will be typically rissoid in character. The rissoid genera *Lironoba* and its subgenus *Nobolira* Finlay, 1926 are only superficially similar, having very different teleoconch and protoconch features when compared in detail. Ponder (1967) has described the radula of a species of *Nobolira*. *Liratoniella* is an eatoniellid with a different operculum which has an opaque muscle insertion area over most of its surface and a typical eatoniellid radula. *Estea crassicarinata* Powell, 1936, tentatively placed in *Liratoniella* by Ponder (1965c) on shell characters, agrees more closely with the type species of *Captitonia*.

### **Eatonina (Captitonia) lirata** sp. nov.

Figs 4a; 15l, m

Derivation of name: *liratus* (Latin) = ridged.

DESCRIPTION. *Shell.* Minute, conical, solid, nonumbilicate, with very strong spiral carinae; orange-brown. Protoconch of 1½ whorls, apex rounded, last whorl stepped; teleoconch of 2½ lightly convex whorls, each with 2 strong, rounded, spiral carinae, with two additional weaker carinae on base and another just abapical to suture, this latter carina becoming prominent on body whorl. Aperture subcircular, inner lip narrow, separated from base in abapical portion; outer lip opisthoclinal; suture bent abapically just abaperturally to outer lip. Colour dark orange-brown, fading to yellowish-brown in dead material, although carinae remain darker.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.00 mm | 0.64 mm |
| Paratype | 1.08 mm | 0.66 mm |

*Operculum.* Typical of genus but with very weak internal ridge (fig. 15l).

*Radula.* Central tooth with weakly convex upper edge with a small thickened area at apex; inner face with very weak, short horizontal ridge-like thickening; lateral folds well developed, curved. Lateral teeth with prominent knob-like swelling on upper inner edge, a massive main cusp immediately below; a small cusp on either side of main cusp and a weak denticle about half way along tooth. Inner marginal teeth with 1 long, sharp cusp with a small cusp on either side. Outer marginal teeth short, with 3 cusps (fig. 15 m).

Operculum and radula examined from type locality (SEM stub no. 337).

TYPES. Holotype (C. 106206) and 7 paratypes (C. 106207), 6 paratypes (C. 106208), AM; 2 paratypes (WAM 395-77), WAM; 1 shell, 1 operculum and 1 radula (SEM stub no. 337).

TYPE LOCALITIES. Garden Is., off Fremantle, W.A., shell sand, 9 Sept. 1972, coll. J. Hewitt (C. 106206, C. 106207). S.W. end of Garden Is., off Fremantle, W.A., on algae, 0-3 m, 21 Jan. 1972, coll. W. F. and J. M. Ponder, B. R. Wilson and N. Coleman (C. 106208).

ADDITIONAL MATERIAL EXAMINED. *S.W.A.:* Ellensbrook ( South Cowaramup), near Margaret River mouth (1). Quininup (11). Yallingup, on algae on limestone platform (1). *W.A.:* S.W. side of Pt. Peron, S. of Fremantle, 3.5 m (1). Bathurst Pt., Rottnest Is. (4).

DISTRIBUTION AND HABITAT. Margaret River to Fremantle and Rottnest Is., Western Australia, living on algae in the sublittoral off Garden Island locality, all other material dead specimens (fig. 22).

REMARKS. This species differs from the New Zealand *Eatonina (? Captitonia) crassicarinata* (Powell) in its smaller size and relatively broader spire.

### Subgenus **Coriandria** Tomlin, 1917:221, nom. nov. pro *Microsetia* Monterosato, 1884a: 280, non Stephens, 1829.

Type species (subsequent designation, Crosse, 1885: 140): *Rissoa cossurae* Calcara, 1841.

Synonyms

*Minosetia* Crosse, 1885b: 148, err. pro *Microsetia*.

*Cingulopsis* Fretter & Patil, 1958: 114.

Type species (original designation): *Cingulopsis fulgida* (J. Adams, 1797) = *Helix fulgidus* J. Adams, 1797).

? *Globisetia* Nordsieck, 1972: 155.

Type species (original designation): *Putilla (Globisetia) globulina* (Monterosato, 1884) = *Setia globulinus* Monterosato, 1884.

DIAGNOSIS. Shell as for genus; usually uniformly coloured, sometimes banded. Operculum as for genus. Radula like that of *Eatonina* s.s. but lacks any denticles on inner faces of central teeth, typically with a pair of cusps on cutting edge; lateral teeth usually with evenly convex upper edge and about 4 subequal cusps, a weak "denticle" on inner face; inner marginal teeth with 3 rather long cusps (sometimes a small fourth cusp present); outer marginal with about 4 cusps. Animal with female genital system diaulic.

DISTRIBUTION. Europe and the Mediterranean Sea; southern Australia.

REMARKS. The radular, shell, opercular and head-foot characters of the type species of *Cingulopsis* and *Coriandria* have been examined and, as already indicated by Nordsieck (1972) on shell characters, they appear to be so similar that they may be considered consubgeneric (figs 5j-m; 11g-n).

Wenz (1943) lists *Coriandria* as a synonym of *Rudolphosetia* Monterosato, 1917 but Nordsieck (1972) maintains them as full genera within the "Coriandridae". Examination of "cotypes" of the type species of *Rudolphosetia (Truncatella? fusca* Philippi, 1841) held in the BMNH (1911.10.26. 24362-24381), shows it to be a member of the Rissoidae as judged on shell, radular and opercular characters. The genus-group taxon *Globisetia* was introduced as a subgenus of *Putilla* A. Adams in the Rissoidae. Paratypes of the type species *(globulina* (Monterosato)) in the BMNH show it to be virtually inseparable in shell characters from *Eatonina (C.) fulgida* and consequently *Globisetia* is tentatively regarded as a synonym of *Coriandria*.

When Tomlin (1917) introduced the name *Coriandria* in a note entitled "New name for *Microsetia* (preoccupied)" he stated "I now propose the new generic name *Coriandria* for the shell I described as *Microsetia durbanensis*". Thus it could be construed that Tomlin intended *durbanensis* to be the type of his new genus, but it has been generally interpreted that Tomlin intended *Coriandria* as a replacement name for *Microsetia* as Barnard (1963) has indicated. Tomlin (1923) when listing *Coriandria durbanensis* states "For the generic name, *vice Microsetia* preoccupied, see . . ." This clearly indicates that Tomlin himself did intend *Coriandria* as a replacement name, as the title of his former article also indicates. Connolly in the "Zoological Record" for 1917 (published 1919) lists *durbanensis** as the type of *Coriandria*. The ICZN Article 67 (i) states that "if a zoologist proposes a new generic name expressly as a replacement for a prior name, both nominal genera must have the same type-species . . ." We concur with Barnard (1963) that *Coriandria* was only intended as a replacement name and will thus have the same type species as *Microsetia*. The first type designation for *Microsetia* was that of Crosse (1885a), not of Monterosato (1884b) as given by Barnard (1963).

Monterosato introduced his new name *Microsetia* almost simultaneously in separate publications (1884a, 1884b). Tomlin (1931:118) has shown that the part of the *Naturalista Siciliano* (1884a) in which *Microsetia* was introduced appeared before the other publication (1884b), which Wenz (1943) gives as the prior one.

Crosse (1885a, b) lists the new names introduced by Monterosato in both publications although the *Nomenclatura* (Monterosato, 1884b) was missed by the Zoological Record until 1900. In listing these names Crosse, possibly inadvertently, made the first type species selections for some of the generic names, including *Microsetia*. In his list of Monterosato's new names in the *Naturalista Siciliano* (Crosse, 1885b) Crosse misspells *Microsetia* as *Minosetia* but as this is clearly an error it cannot be used as a replacement name for *Microsetia* Monterosato (ICZN Art. 33(b)).

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* Examination of the type material of *Coriandria durbanensis* in the BMNH indicates that this species is not a cingulopsid but it possibly belongs in the Hydrobiidae.

Two Southern Australian species are here included in *Coriandria*, mainly on the basis of their considerable similarity in radular features with their northern hemisphere counterparts. It is possible that these similarities are due to convergence but they may equally well reflect the remnants of a Tethyan distribution.

### **Eatonina (Coriandria) fulvicolumella** sp. nov.

Figs 3h; 11a-d

Derivation of name: *fulvus* (Latin) = brown, *columella* (Latin) = a little column; refers to the brown columella of the shell.

DESCRIPTION. *Shell*. Minute, ovate-conical, moderately solid, smooth, opaque, very narrowly umbilicate, pale yellowish-brown, with dark brown columella and umbilical area. Protoconch of 1½ smooth whorls; teleoconch of 2½ very weakly convex whorls, smooth except for growth lines and weak spiral scratches. Periphery slightly subangled. Aperture almost circular, lips thin, inner lip narrow, edge straight, abapical portion separated from base as a thin lamella; outer lip moderately prosocline. Suture bent slightly abapically on abapertural side of outer lip. Umbilicus very narrow, sometimes closed leaving only a distinct umbilical chink. Colour yellow-brown or very pale yellow-brown to almost dirty white, middle base with a very faint, narrow brown band, stronger within aperture, umbilical area and columella dark brown.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.15 mm | 0.75 mm |
| Paratype | 1.11 mm | 0.76 mm |
| Figured specimen<br>Paratype (SEM stub no. 385) | 1.14 mm | 0.76 mm |

*Operculum*. Typical of genus (fig. 11b).

*Radula*. Typical of subgenus; central tooth having almost straight upper edge with a small knob-like swelling in middle and two broad, rounded cusps; lateral folds prominent. Lateral teeth with 4 cusps, middle rather large, inner-most cusp with 3-4 filament-like structures (easily worn off as in fig. 11c). Inner marginal teeth with 4 cusps, middle 2 large, third cusp largest, first and fourth cusps small. Outer marginal teeth with 3 sharp cusps and a denticle (fig. 11d).

Operculum and radula examined from type locality (SEM stub no. 385) and Goat Is., N. Tasm. (SEM stub no. 531).

TYPES. Holotype (C. 106195) and 8/3w paratypes (C. 106196), AM; 2 paratypes (E9816), TM; 1 shell, 2 opercula and 2 radulae (SEM stub no. 385).

TYPE LOCALITY. Great Taylor Bay, South Bruny Is., Tasm., 7.6 m, on algae, sandy bottom, 14 Feb. 1973, coll. N. Coleman.

ADDITIONAL MATERIAL EXAMINED. *N.S.W.*: N. side of Black Head, Nadgee, coralline algae, exposed rocks (2). *Tasm.*: Goat Is., near Ulverstone, on coralline algae (1). Wedge Bay, 13 m (4). Nubeena, Tasman Peninsula, 7 m (1). *S.A.*: Pearson Is., Investigator Group, 18 m, on algae (2).

DISTRIBUTION AND HABITAT. Southern New South Wales, Tasmania to South Australia, in the sublittoral living on algae (fig. 22).

REMARKS. This species is easily distinguished from other Australian species of the family by its pale, rather conical shell with its dark columella and umbilical area. It is, however, very similar to "*Rissoa atkinsoni* T. Woods" with which it occurs sympatrically. The general coloration of *R. atkinsoni* is very similar, including the pale brown band on the base, but differs in having a second band bordering the otherwise pale umbilical area. The inner lip is less heavily pigmented in *R. atkinsoni*, the whorls are more convex and the shell lighter in build. It will be shown elsewhere that *R. atkinsoni* is correctly placed in the rissoid genus *Lucidestea* Laseron, 1956 (Ponder and Yoo, in preparation).

*Eatonina (E.) condita* nov. is sympatric with *E. (C.) fulvicolumella* and the shells of these two species are very similar in shape and size but can be distinguished by the uniform dark brown coloration of *E. (E.) condita* and the more distinctly prosocline outer lip of *E. (C.) fulvicolumella.*

### **Eatonina (Coriandria) rubicunda** sp. nov.

Figs 3i; 11e, f.

Derivation of name: *rubicunda* (Latin) = ruddy, red; refers to the colour of the shell.

DESCRIPTION. *Shell.* Minute, ovate-conical, solid, opaque to subopaque, smooth, with rather dull surface, nonumbilicate to very narrowly umbilicate, dark red-brown. Protoconch of 1½ whorls (surface worn); teleoconch of 2½ convex whorls, sculptured with fine growth lines and very indistinct spiral scratches. Aperture subcircular to circular, inner lip narrow, with slightly concave edge, raised above base in abapical portion. Outer lip thin, slightly prosocline; suture inclined slightly abapically a little abaperturally to edge of outer lip where a very weak varix formed. Colour dark red-brown, inner rim of aperture and umbilical area very dark, a narrow yellowish-brown zone abaperturally to outer lip.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.22 mm | 0.83 mm |
| Paratype | 1.33 mm | 0.90 mm |
| Figured specimen<br>Paratype (SEM stub no. 424) | 1.28 mm | 0.91 mm |

*Operculum.* Not examined.

*Radula.* Typical of subgenus; central tooth with 2 close-set, blunt cusps and prominent lateral folds; upper edge strongly convex, a weak, knob-like swelling in middle. Lateral teeth with 4 long, sharp cusps, innermost with 2 filament-like processes. Inner marginal teeth with 4 sharp cusps, second and third cusps long; two supporting structures, innermost small. Outer marginal teeth with 4 sharp cusps, outermost small (fig. 11f).

Radula examined from type locality (SEM stub no. 424).

TYPES. Holotype (C. 106197) and 4 paratypes (C. 106198), AM; 1 paratype (D15981), SAM; 1 shell and 2 radulae (SEM stub no. 424).

TYPE LOCALITY. Elliston, S.A., 0-5 m, on algae, Feb. 1974, coll. V. Taylor.

DISTRIBUTION AND HABITAT. Known only from the type locality in South Australia where it lives on lower littoral and sublittoral algae (fig. 22).

REMARKS. The shell of *E. (C.) rubicunda* is similar to that of *E. (E.) sanguinolenta* nov. but *sanguinolenta* has a relatively taller spire, a more glossy surface, is more translucent and has a relatively paler inner lip. *Eatonina (E.) shirleyae* nov. is very similar to *E. (C.) rubicunda* in the general appearance of the shell but it has a relatively paler inner lip, less convex whorls and a more strongly prosocline outer lip. *Eatonina (E.) rubrilabiata* nov. is also somewhat similar in shell features to *E. (C.) rubicunda* but is paler and more orange than red, has a slightly taller spire, a relatively smaller body whorl and aperture, and the outer lip is orthocline, not prosocline. All of these species markedly differ from *E. (C.) rubicunda* in radular features.

### Subgenus **Mistostigma** Berry, 1947: 9 (265)

Type species (original designation): *Mistostigma punctulum* Berry, 1947 = ? *Cithna orvieta* Dall, 1919 = *Cythnia albida* Carpenter, 1864.

DIAGNOSIS. Shell broadly ovate, umbilicate, uniform brown in colour. Operculum as for genus. Radula similar to that of *Eatonina* s.s. except central tooth bears 3 prominent cusps on cutting edge (in type species), lateral folds weak and with 2 pairs of denticles on inner face. Lateral teeth with 2 denticles on inner face. Animal unknown.

DISTRIBUTION. Pacific coast of North and South America.

REMARKS. The types species was originally described as a Pliocene fossil from Bath-house Cliff, Santa Barbara, California. Paratypes have been examined in the San Diego Museum of Natural History and these agree closely with Lower Pleistocene specimens from the Lomita Formation, San Pedro, California and Recent specimens held by the Los Angeles County Museum of Natural History (figs 14 a, b,). Dr J. H. McLean has pointed out to us *(in litt.)* that the name *Cythnia albida* Carpenter is probably the earliest one for the species and that *Cithna orvieta* Dall is probably another synonym. Palmer (1958) has figured Carpenter's type specimen which is held in the NMNH (No. 15569).

*Eatonina atacamae* Marincovich from Chile is here placed in *Mistostigma* although the cusps on the central tooth are very reduced and the two pairs of denticles are more strongly developed than in the type species. In most respects the central teeth are more like those of some species of *Eatonina (Eatonina)* but the lateral teeth each have two weak denticles on their inner face, 4 rather uniformly-sized cusps and a slightly humped upper margin (figs 14 h-i).

### Subgenus **Otatara** Ponder, 1965a: 120

Type species (original designation): *Notosetia subflavescens* Iredale, 1915 (nom. nov. pro *Rissoa atomus* Suter, 1908, non Smith, 1890).

DIAGNOSIS. Shell and operculum similar to that of *Eatonina* s.s. but radula with a single cusp on each lateral tooth and inner and outer marginals unicuspid.

DISTRIBUTION. North eastern New Zealand and the Bounty Islands.

REMARKS. This subgenus is tentatively retained because of the recorded radular features. It is, however, possible that the re-examination of the radula of *Eatonina subflavescens* using the SEM will indicate that there are insufficient differences to retain subgeneric status. Another possible problem is the considerable distance between the type locality of *N. subflavescens* and the material examined by Ponder (1965). There is considerable difficulty experienced in separating species on shell characters in this group and the status of the subgenus cannot be fully determined until the radula of specimens from the Bounty Islands is examined.

## Genus **Eatoniopsis** Thiele, 1912: 237

Type species (monotypy): *Eatoniella paludinoides* Smith, 1902.

DIAGNOSIS. Shell minute, ovate-conical to depressed-trochoid, smooth, umbilicate or non-umbilicate. Protoconch smooth, of about 1½ whorls. Aperture subcircular, columella usually almost straight, with a distinct, low bulge which renders its free edge slightly convex. Usually uniformly coloured. Operculum rather thin, flexible, transparent, yellowish, with a short, curved peg extending beyond the margin; no internal ridge. Radula with small central teeth, subtriangular lateral teeth and long, curved marginal teeth; marginal and lateral teeth all multicuspate, central teeth with lateral folds, each usually with a relatively large, simple, blunt, easily shed cusp. Head foot typical of family.

DISTRIBUTION. Antarctica, New Zealand, Australia and New Hebrides.

REMARKS. *Boogina* Thiele, *Rufodardanula* Ponder and *Eatoniopsis* Thiele have been regarded by Ponder (1965) as sufficiently distinct to allow them full generic status. However, the examination of the radulae of a number of species of *Eatoniopsis s.l.* has shown that the cusp pattern and shape of the teeth, although falling into these three groups, are sufficiently similar to allow only subgeneric distinction. An additional subgenus *(Pilitonia* nov.) is described below which, unlike the other three subgenera, also has a distinctive shell. *Tubbreva* Ponder, regarded by Ponder (1965a) as a subgenus of *Rufodardanula,* is here given generic status.

The central teeth of most of the observed species of this genus have a large, blunt, cusp-like structure which is uniquely difficult to clean in mounts and which is easily shed. Specimens lacking this structure on all or some of the central teeth in the ribbon have a shallow socket indicating its positon. It is probable that this cusp is chemically or structurally different from the rest of the radula.

### KEY TO SUBGENERA OF *EATONIOPSIS*

1. Shell ovate-conic .......... 2
   Shell depressed trochiform .......... *Pilitonia*
2. Central teeth of radula with vertical structures on face of teeth; lateral teeth with numerous cusps subequal in size .......... 3
   Central teeth of radula without vertical structures on face of teeth; lateral teeth with few cusps, 1-2 much larger than others .......... *Eatoniopsis* s.s.
3. Central teeth with 1-3 strong vertical structures on face of teeth, lateral folds usually well developed .......... *Rufodardanula*
   Central teeth with 1-2 weak, vertical structures on face of teeth, lateral folds weak .......... *Boogina*

### KEY TO THE AUSTRALIAN AND TROPICAL INDO-PACIFIC SPECIES OF *EATONIOPSIS*

1. Shell ovate-conic .......... 2
   Shell depressed trochiform .......... 4
2. Shell brown .......... 3
   Shell white with brown protoconch .......... *E. (R.) porcellana* nov.
3. Shell narrowly umbilicate, 1.4 mm or longer .......... *E. (B.) voorwindei* nov.
   Shell not umbilicate, less than 1.4 mm long .......... *E. (R.) castanea* (Laseron)
4. Shell pale orange-brown with brown band on shoulder .......... *E. (P.) westralis* nov.
   Shell yellowish-white, with 2 narrow brown bands .......... *E. (P.) translucida* nov.

### Subgenus **Eatoniopsis** s.s.

DIAGNOSIS. Shell as for genus, ovate-conical, non-umbilicate or narrowly umbilicate. Operculum as for genus. Radula with central teeth lacking any structures on the face apart from lateral folds and a short, broad, simple to weakly bifid cusp; lateral teeth with few cusps, one cusp (second or third from inner end) much larger than others; inner marginal slightly longer than outer marginal tooth, both with relatively few cusps, inner marginal with at least one cusp much longer than others (figs 13j-n).

DISTRIBUTION. Antarctica.

REMARKS. This subgenus is distinguished by the radula having simple central teeth and conspicuously unequally developed cusps on the lateral and inner marginal teeth. The peculiar, cusp-like structure seen in the other species of *Eatoniopsis* appears to be represented in *E. paludinoides* by a weakly bifid cusp (figs 13m, n) which is much shorter than any of the other species of the genus. A second species of *Eatoniopsis* from Antarctica, probably attributable to *Rissoa edwardiensis* Watson, 1886 (figs 13 f-i) is very like *E. paludinoides* in radular features except for the central teeth which have a large cusp like that of other species of the genus (figs 13h, i).

### Subgenus **Boogina** Thiele, 1913: 86.

Nom. nov. pro *Watsoniella* Thiele, 1912: 237, non Berg, 1898.

Type species (original designation): *Rissoa (Setia) sinapi* Watson, 1886.

DIAGNOSIS. Shell ovate-conical to ovate, very narrowly umbilicate, otherwise as in generic diagnosis. Operculum as in generic diagnosis. Radula with central teeth each bearing 1-2 weak, vertical structures with weak lateral folds, cusp large, on narrow neck. Lateral teeth with inner edge slightly extended, cusps all small, numerous. Inner marginal teeth long with 1 long and several short cusps; outer marginal teeth long, multicuspate.

DISTRIBUTION. Subantarctic (Kerguelen Is.); temperate Australia.

REMARKS. The specimens on which Thiele based his genus name have been destroyed by corrosion and are completely unidentifiable (Humbolt Universität Museum, No. 63066). The figure given by Thiele (1912, pl. 15, fig. 2) does not agree very closely with that given by Watson (1886, pl. 45, fig. 13). Watson's figure shows a slightly higher spire and neither the figure nor the description indicates the columellar bulge which is distinctive in Thiele's figure, although a weak bulge is present in the two syntypes in the BMNH. One syntype is a juvenile and the other a larger, doubtfully adult, specimen (reg. no. 87.2.9.2020-1). The larger specimen (1.05 mm in length) is here designated the lectotype as it clearly represents the basis of Watson's description and figure. Until a series of topotypes of *Eatoniopsis (Boogina) sinapi* can be examined and the shell variation and radular structure assessed the question of the actual identity of Thiele's specimens must remain in some doubt.

### **Eatoniopsis (Boogina) voorwindei** sp. nov.

Figs 4g; 13a-e

DESCRIPTION. *Shell.* Minute, ovate-conical, translucent, smooth and shining, narrowly umbilicate, pale orange-brown. Protoconch of 1½ whorls; teleoconch of about 3 convex whorls, smooth except for exceedingly fine spiral scratches and indistinct axial growth lines. Suture false-margined. Aperture subpyriform; inner lip thin over parietal wall, thicker and slightly separated from base in abapical portion. Columella with distinct, broad bulge; outer lip thin, simple. Umbilicus narrow, partly hidden by inner lip. Colour pale orange-brown, umbilical area and inner lip slightly darker.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.56 mm | 1.06 mm |
| Paratype | 1.53 mm | 1.01 mm |
| Figured specimen | | |
| Paratype (SEM stub no. 432) | 1.42 mm | 1.00 mm |

*Operculum.* Typical of genus (fig. 13b).

*Radula.* Typical of subgenus; central tooth with 0-2 weak vertical processes which are suspended from the arched middle face of each tooth; cusp square, sometimes weakly bifid. Lateral teeth with about 18 short, sharp cusps which gradually decrease in size towards outside. Inner marginal teeth with a large distal "cusp" and about 4-6 small, sharp cusps on either side. Outer marginal teeth with several small, sharp cusps on either side (figs 13c-e).

Operculum and radula examined from type locality (SEM stub no. 432).

TYPES. Holotype (C. 106214) and 2/1w paratypes (C. 106215), AM; 1 shell, 1 operculum and 1 radula (SEM stub no. 432).

TYPE LOCALITY. S. side, tip of Green Cape, N.S.W., on vertical rock faces, 16 m, Feb, 1973, coll. S.A. Shepherd.

ADDITIONAL MATERIAL EXAMINED. *N.S.W.*: Fingal Bay, Port Stephens (1). Narrabeen, Sydney (4). Off Chinamans Beach, Middle Harbour, Sydney, 4-7m (7). Off Sow and Pigs Reef, Sydney Harbour, dredged (1). Little Coogee Bay, Sydney (2). Ocean beach, Kurnell, Botany Bay (1). Ocean beach, Cronulla (1). Ulladulla (1). S. end of Green Cape, 2-4 m on algae, exposed coast (1); 16 m on algae on vertical rock faces (4). *Tasm.:* Murray Pass., Deal Is., Bass Strait, 30-50m, on red algae (1).

DISTRIBUTION AND HABITAT. Port Stephens, New South Wales, to Bass Strait, on algae in the lower littoral and sublittoral (fig. 23).

REMARKS. *Eatoniopsis (Boogina) voorwindei* differs from *Eatoniopsis (Rufodardanula) castanea,* with which it is sympatric, in its larger size, thinner, more translucent shell, paler colour, its umbilicus and its more convex whorls.

This species is only the second known *Boogina,* the shell differing from the type species from Kerguelen Is. by its larger size and more prominent columellar bulge.

This species is named for Mr J. Voorwinde of Sydney as a small mark of appreciation for the many services which he has rendered us in the course of this work.

### Subgenus **Rufodardanula** Ponder, 1965a: 124.

Type species (original designation): *Rufodardanula spadix* Ponder, 1965.

DIAGNOSIS. Shell ovate-conical, non-umbilicate, otherwise as in generic diagnosis. Operculum as in generic diagnosis. Radula with central tooth bearing a prominent, easily shed, simple or weakly bifid cusp which is sometimes raised above body of tooth by a short neck; face of each tooth with 1-3 strong vertical ridges and strong to weak lateral folds. Lateral teeth multicuspate, cusps all small, sharp and numerous; inner and outer marginal teeth long, of similar size, curved, multicuspate, inner marginal teeth with one cusp longer than others, outer marginal teeth with several small cusps.

DISTRIBUTION. New Zealand and eastern Australia.

REMARKS. *Rufodardanula* is very similar to *Boogina* in shell, radular and opercular characters. The central teeth differ, however, in that the very strong, median pillar-like vertical thickening and the thick lateral folds seen in the type species of *Rufodardanula* (and one of the 2 Australian species described herein) are represented in Thiele's drawing (1912, pl. 15, fig. 25) of *Eatoniopsis (Boogina) sinapi* as only 3 small denticles. In addition the lateral teeth have considerable extensions on the lower part of the inner edge in *Rufodardanula spadix* (figs 12j-l) which do not occur in *Eatoniopsis (Boogina) sinapi*, nor in *E. (Boogina) voorwindei* nov. There do not appear to be intermediate situations encountered in the radulae of the species described herein.

### **Eatoniopsis (Rufodardanula) castanea** (Laseron, 1950)

Figs 4b; 5i; 12a-e.

*Notosetia castanea* Laseron, 1950: 281, fig. 78.

DESCRIPTION. *Shell.* Minute, ovate-conical, semitranslucent, smooth and shining, nonumbilicate, dark to medium orange or red-brown. Protoconch of 1½ whorls; teleoconch of up to about 2¼ weakly convex whorls, smooth except for rather distinct axial growth rugae and exceedingly fine spiral scratches. Suture distinctly false-margined. Aperture sub-pyriform; inner lip thin over parietal wall, broader and separated from base in abapical portion. Columella with weak, broad bulge, outer lip thin, simple. Umbilical chink present but no umbilicus. Colour uniform dark orange to red-brown, sometimes paler orange-brown with darker inner lip and umbilical area.

Dimensions

| | Length | Diameter |
|---|---|---|
| Lectotype | 1.30 mm | 0.88 mm |
| Paralectotype | 1.16 mm | 0.80 mm |
| Figured specimen | | |
| Fairlight, Sydney, N.S.W (SEM stub no. 137) | 1.18 mm | 0.77 mm |

*Operculum.* Typical of genus (figs 12b, c).

*Radula.* Typical of subgenus; central tooth with blunt, rather narrow cusp, a prominent median vertical ridge extending just beyond face of tooth and two lateral vertical ridges; narrow outgrowths of lateral ridges may represent weakened lateral folds. Lateral teeth with 11-13 small, sharp cusps, and a blunter cusp (innermost), all gradually decrease in length outwards. Inner marginal cusp with about 8 small sharp cusps on outside of long median cusp, at least 1 on inside (number not determinable from available photographs). Outer marginal teeth with small, sharp cusp (number not determinable) (figs 12d, e).

Opercula and radulae examined from Nambucca Heads, N.S.W. (SEM stub no. 134) and Fairlight, Sydney, N.S.W. (SEM stub no. 137).

*Head-foot.* Snout short, bilobed, tentacles rather long, constantly lashing up and down. Foot bluntly rounded in front, sharply rounded behind. Posterior mucous slit long, extending about two-thirds of length of foot, posterior mucous gland and anterior mucous gland denser whitish than rest of semitransparent white foot; opercular lobes white (Long Reef and Fairlight, Sydney) (fig. 5i).

TYPES. Lectotype (C. 105674) (here chosen) and 3 paralectotypes (C. 105675), AM.

TYPE LOCALITY. Middle Harbour, Sydney, N.S.W., on *Galeolaria*.

ADDITIONAL MATERIAL EXAMINED. *Qld.*: Amity Pt., North Stradbroke Is., 0-4 m, on algae (1). *N.S.W.*: N. tip of Cape Byron, on algae, sheltered side (16). Ballina, on algae (4). Nambucca Heads, coralline algae (17/8w). Forster (2); green algae, low tide (1). Fingal Bay, Port Stephens (24). Off Patonga Beach, Broken Bay, dredged (4). Pittwater, Broken Bay, dredged (2). Narrabeen, Sydney (3). Collaroy, Sydney (5). N. side Long Reef, Collaroy, Sydney, coralline algae, semi-exposed platform, low tide (2). Long Reef, Collaroy, Sydney, on algae (11). N.E. side Long Reef, Collaroy, Sydney, under stones (6); on algae (5); coralline algae in pool, low tide (1). S. side of Long Reef, Collaroy, Sydney, on algae in pool, low tide (4). Harbord, Sydney, below R.S.L. Club, 10 m, rock washings (1w). Ocean beach, Manly, Sydney (10). S.E. side of Reef Beach, Sydney (4). North Harbour, Sydney, dredged (20). Fairlight, Middle Harbour, Sydney, on *Zonaris* (7); coralline algae (9); mixed short algae (19/10w); amongst *Galeolaria* (2); under stones (5w). Near Fairlight Pool, Middle Harbour, Sydney, coralline algae (17). Wyargine Pt., Middle Harbour, Sydney, on algae (1w). Off Chinamans Beach, Middle Harbour, Sydney, 5 m (15). Balmoral, Middle Harbour, on algae (3w); on brown algae (3w); 18 m, dredged (2); on coralline and red algae, 1-2 m, N. end (3w). Off Sow and Pigs Reef, Middle Harbour, Sydney, 9 m, dredged (4). Parsley Bay, Sydney, 3 m on green algae (1). Ocean beach, Kurnell, Botany Bay (2). Gunnamatta Bay, Port Hacking (1). Shell Harbour, on algae (2). Honeymoon Beach, Jervis Bay, on algae, low tide (1). Wreck Bay, just S. of Jervis Bay, 4.5 m, on coralline algae (13). Inside breakwater, S. side of Ulladulla, on small brown algae, sheltered reef (2); on coralline algae (14/4w). Outside breakwater, S. side of Ulladulla, on coralline algae, moderately exposed rock platform (3). On seaward side of long rocky point, Batehaven, Batemans Bay, on red algae, medium exposure (4). Wimbie Beach, Batemans Bay, on fairly exposed rocky shore, under stones (4); on large brown algae (12); on coralline algae (4). Shelly Beach, Bermagui (21). Eden Harbour (2). Eden, Twofold Bay, 10 m, on coralline algae (5). Bitangabee, N. side of Green Cape, 15 m, between rocks (2); below lighthouse, on algae, low to mid-tide (2). *Tasm.*: Murray Pass., Deal Is., Bass Strait, 30-50 m, on red algae (1). Boat Harbour, under stones (2). Goat Is., near Ulverstone, on coralline algae (1); under stones (1). Roches Beach, Frederick Henry Bay, on short brown algae, on semisheltered reef (2). Primrose Pt., Frederick Henry Bay, on coralline algae, in pool, low tide (1); matted green algae, low tide (1). *Vic.*: Monumental Bay, Gabo Is., 15-18 m, on algae (1). Bastion Pt., S. tip of Mallacoota, intertidal (13).

DISTRIBUTION AND HABITAT. North Stradbroke Is., S. Qld, to Tasmanina and eastern-most Victoria, on algae, stones and debris in the mid to lower littoral and sublittoral; often abundant (fig. 23).

REMARKS. This species is distinguished from the other two species of the subgenus by its uniform brown colour and evenly-conical form. It is one of the commoner minute molluscs living on algae in New South Wales and is readily distinguished from other species living with it by its rather conical shell, the bulge on the columella and its orange-brown colour.

### **Eatoniopsis (Rufodardanula) porcellana** sp. nov.

Figs 4c; 12f-h.

Derivation of name: porcelain-like.

DESCRIPTION. *Shell.* Minute, ovate-conical, semitransparent, smooth, white with pale brown protoconch, nonumbilicate. Protoconch of 1½ whorls; teleoconch of 2½ weakly convex whorls, smooth except for weak growth lines. Aperture pyriform, angled in adapical corner; inner lip thickened, narrow, edge nearly straight, columella with a prominent bulge, abapical portion a little separated from base; outer lip thin, straight, prosocline. Suture bent abapically just abaperturally to outer lip. Umbilical chink very minute to absent. Colour of protoconch (and sometimes first whorl of teleoconch) very pale brown to translucent white, other whorls translucent white with a broad white band abapical to suture and white in umbilical area, sometimes two narrow brown lines on base.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.06 mm | 0.67 mm |
| Paratype | 1.04 mm | 0.65 mm |
| Figured specimen<br>One Tree Is., Qld (SEM stub no. 463) | 0.92 mm | 0.60 mm |

*Operculum.* Typical of genus (figs 12g, i).

*Radula.* Similar to that of *E. (R.) castanea* but with narrower, more triangular central tooth, lateral folds prominent with only a trace of vertical ridges under and below them; cusp not present in specimen examined and presumed shed. Lateral teeth with about 11 cusps gradually decreasing in size outwards. Inner marginal teeth with about 5 sharp cusps outside long median cusp, with at least 1 (probably more) cusps on inside. Outer marginal teeth finely cuspate (fig. 12h).

Operculum and radula from One Tree Is., Qld (SEM stub nos 263 & 463).

*Head-foot.* Translucent, nonpigmented.

TYPES. Holotype (C. 106209) and 18 paratypes (C. 106210), AM; 2 paratypes (MO 6316), QM.

TYPE LOCALITY. 3km E. of Heron Is., Qld, on algae on coral 'bommie', in middle of lagoon, 1-2.5m, 30 Dec. 1976, coll. W. F. Ponder.

ADDITIONAL MATERIAL EXAMINED. *Qld:* S.W. corner of Heron Is., Capricorn Group, on rubble with green filamentous algae, below beach (1). S. outer face, One Tree Is., Capricorn Group, 1-5m (11/4w).

DISTRIBUTION AND HABITAT. Heron Is. and One Tree Is., Capricorn Group, Southern Barrier Reef, Queensland, on algae and algal covered rubble in the lower littoral and sublittoral (fig. 23).

REMARKS. This species can be distinguished from the others in the genus by its lack of pigmentation and by the rather thick inner lip. It superfically resembles some minute species of *Eatoniella* but the shell can be distinguished by the bulge on the columella.

Three specimens tentatively associated with this species are similar in shape, a little smaller in size (largest specimen 0.81 x 0.54 mm), dark purplish-brown with a white aperture (fig. 4d). They probably represent an undescribed species but the shells are in rather poor condition and an assessment of their status should await the availability of additional material. The available material was collected on the south side of Heron

Island (opposite the Research Station) over the edge of the reef in 2m on coral rubble with an algal coating (26 Dec. 1976, coll. W. F. Ponder) (AM, C. 106212). One specimen was destroyed and provided an SEM mount (stub no. 478) of the operculum (fig. 12i), which closely resembles that of *E. porcellana,* but the radula was not successfully mounted.

### Subgenus **Pilitonia** nov.

Type species: *Eatoniopsis (Pilitonia) westralis* sp. nov.

Derivation of name: *pila* (Latin) = a ball.

DIAGNOSIS. Shell minute, depressed-trochiform, narrowly umbilicate, smooth. Aperture oval, inner lip thin, narrow, convex, columella concave, with weak bulge, outer lip thin, simple. Operculum typical of genus. Radula with central tooth ∩-shaped bearing a weak, median, vertical structure probably representing a reduced cusp, and two lateral thickenings, no true cusps; lateral and marginal teeth as in *Eatoniopsis (Rufodardanula)* except that the lateral teeth have an even more pronounced inwards extension of their lower inside margin and this bears a few blunt cusps. Animal not known.

DISTRIBUTION. Western Australia, South Africa and the New Hebrides.

REMARKS. The three known species of this subgenus are readily distinguished from those of other subgenera of *Eatoniopsis* by the depressed spire of the globose shell. The cuspate inner extension of the lateral teeth and the shape of the central teeth of the radula are also distinctive, and the central teeth appear to lack the deciduous cusp seen in the other subgenera. In general, however, the radula and operculum are similar to *Eatoniopsis,* and in particular the subgenus *Rufodardanula,* and the shell is also similar in having a bulge on the columella. For these reasons the differences are here considered to be of subgeneric value only. Two species are described herein and a third undescribed species is known from South Africa (East London).

### **Eatoniopsis (Pilitonia) translucida** sp. nov.

Figs 4e; 15a, b.

Derivation of name: *translucidus* (Latin) = transparent, translucent.

DESCRIPTION. *Shell.* Minute, depressed-trochiform, thin, translucent, usually umbilicate, yellowish-white with two narrow brown bands. Protoconch of 1½ smooth whorls; teleoconch of 1½ convex whorls, smooth except for fine axial growth lines. Aperture subcircular; inner lip narrow and thin on parietal wall, thick and free over umbilical area (i.e. in abapical portion). Columella with prominent broad bulge; outer lip thin. Umbilicus closed or partly closed by thickened abapical part of inner lip. Protoconch and first whorl of teleoconch pale orange-brown, remainder of shell translucent yellowish-white with a very narrow brown band adapical to periphery and another abapical to periphery, the former visible on penultimate whorl; inner lip white.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 0.60 mm | 0.73 mm |
| Paratype | 0.52 mm | 0.68 mm |
| Figured specimen | | |
| Paratype (SEM stub no. 139) | 0.48 mm | 0.62 mm |

*Operculum.* Typical of genus (fig. 15b).

*Radula.* Mount very poor but in general features similar to that of *E. (P.) westralis* nov.

Operculum and radula examined from type locality (SEM stub no. 139).

TYPES. Holotype (C. 106216) and 4 paratypes (C. 106217), AM; 3 shells, 2 opercula and 2 radulae (SEM stub no. 139).

TYPE LOCALITY. Hotel Tanna, Tanna Is., New Hebrides, on algae on exposed rocks, low tide, 1 Feb. 1967, coll. W. F. Ponder.

DISTRIBUTION AND HABITAT. Known only from the type locality in the New Hebrides where it lives on algae in the lower littoral on an exposed shore (fig. 23).

REMARKS. This species is distinguished from *Eatoniopsis (Pilitonia) westralis* nov. by its paler colour, two brown bands, the thicker, white abapical part of the inner lip and the narrower umbilicus. This species is superficially similar to *Eatonina (Eatonina) heliciformis* but that species differs in its higher spire, different colour pattern and in its simple inner lip.

### **Eatoniopsis (Pilitonia) westralis** sp. nov.

Figs 4f; 15c-g.

Derivaton of name: from Western Australia.

DESCRIPTION. *Shell.* Minute, depressed-heliciform, thin, translucent, widely umbilicate, pale orange-brown with very weak orange-brown band on shoulder. Protoconch of 1½ smooth whorls; teleoconch of up to 2 convex whorls, smooth except for extremely fine spiral scratches and coarser axial growth lines. Aperture subpyriform; inner lip narrow and thin on parietal wall, wider and free across umbilical area; columella with a weak bulge; outer lip thin. Umbilicus wide for family, deep. Colour pale to moderate orange-brown, inner lip and umbilical area darker orange-brown. A faint brown band on shoulder of body whorl usually present.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 0.87 mm | 0.90 mm |
| Paratype | 0.82 mm | 0.82 mm |
| Figured specimen<br>Paratype (SEM stub no. 149) | 0.80 mm | 0.80 mm |

*Operculum.* Typical of genus (figs 15d, f).

*Radula.* As described for subgenus; central tooth with small, blunt, median cusp (?) and 2 rather narrow lateral folds supported by an arched upper surface; face of each tooth reduced to narrow plate, lower edge of which is parallel to dorsal arch. Lateral teeth with convex upper edge and concave lower edge, inner extension about ¼ total length of each tooth, with 4 blunt, short, cusp-like projections; innermost true cusp broad and blunt, of similar length to adjacent cusps, these very narrow, sharp, decreasing in length outwards, 9-10 in number. Inner marginal teeth with large distal cusp and 4 small cusps on outside of each tooth (number on inside not known). Outer margin with few small cusps (details not known) (figs 15e, g).

Opercula and radulae examined from type locality (SEM stub no. 149) and Rottnest Is., W.A. (SEM stub no. 275).

TYPES. Holotype (C. 106219) and 11/1w paratypes (C. 106220), AM; 2 paratypes (D

15983), SAM; 2 paratypes (WAM 396-77), WAM; 2 shells, 2 opercula and 1 radula (SEM stub no. 149).

TYPE LOCALITY. Mississippi Bay, 48km E. of Esperance, S.W.A., on algae, on sheltered side of W. head of bay, 0-2 m, 6 Feb. 1972, coll. W. F. Ponder.

ADDITIONAL MATERIAL EXAMINED. *S.A.*: Tumby Bay (1). Elliston, 0-5m, on algae (2). *S.W.A.:* Yallingup, on algae, on limestone platform (1). Cape Naturaliste (1). *W.A.*, S.W. side of Pt. Peron, S. of Fremantle, 2-3m (1); sandy bottom, low tide (1). S.W. end of Garden Is., off Fremantle (2). Garden Is. (8). W. side Carnac Is., off Fremantle, 4-8m, on algae (11); rubble washings, low tide (3). North Pt., Rottnest Is., on algae, protected reef (39/11w). W. end Salmon Bay, Rottnest Is., *Lithothamnion* washings from reef edge (9). W. end reef, Rottnest Is., *Lithothamnion* washings from intertidal reef edge (1). Near end of Natural Jetty, Rottnest Is., 1m, in crevices of walls of small pools (1w). Triggs, Perth, 0-2m, on coralline algae, on platform, open coast (2). Watermans Beach, Perth (3/2w).

DISTRIBUTION AND HABITAT. Tumby Bay, South Australia to the vicinity of Perth, Western Australia, living on algae and debris in the lower littoral and shallow sublittoral on open coasts (fig. 23).

REMARKS. This species is not similar to any other known species with the exception of the preceding with which it has already been contrasted. It is one of the commoner algae-living minute gastropods in south Western Australia and cannot be confused with any sympatric species.

## Genus **Tubbreva** Ponder, 1965a: 125.

Type species (original designation): *Rufodardanula (Tubbreva) exigua* Ponder, 1965.

DIAGNOSIS. Shell minute, elongately conical, thin, smooth, columella nearly straight, with a weak bulge, nonumbilicate. Operculum thin, oval, lacking an internal ridge, peg very short, not projecting beyond margin. Radula absent. Head-foot typical of family.

DISTRIBUTION. New Zealand, Australia (and Hawaii?).

REMARKS. The type species (figs 15j, k), another New Zealand species *Tubbreva exaltata exaltata* (Powell) and the 2 new species of *Tubbreva* described herein were all examined and it has been confirmed that there is no radula present as was suspected by Ponder (1965a). Because of the absence of a radula and the very short opercular peg, *Tubbreva* is here considered to be sufficiently distinct to be given generic status. This genus is placed in the Cingulopsidae on the basis of the similarity in opercular and shell features to other members of the family. The external features of the head-foot are also very similar to other members of the family (Ponder, 1965a).

An undescribed species from Hawaii (E. A. Kay, pers. comm.) probably belongs in this genus and Ponder (1965a) recognises three species and one subspecies from the New Zealand region.

### KEY TO THE AUSTRALIAN SPECIES OF *TUBBREVA*.

Shell with weakly sinuate outer lip and indistinct spiral bands .*T. insignificans* nov.
Shell with simple outer lip, uniformly pale orange............................*T. parva* nov.

### **Tubbreva insignificans** sp. nov.

Figs 4h, i; 15h.

Derivation of name: *insignificans* (Latin) = insignificant.

DESCRIPTION. *Shell.* Minute, thin, translucent, elongate-conical, nonumbilicate yellowish-brown, with 2 indentations in outer lip. Protoconch of 1½ whorls; teleoconch of 2½ lightly convex, smooth whorls. Aperture oval, outer lip strongly prosocline with 2 weak, broad indentations; inner lip narrow, with concave edge, separated from base at abapical end; columella with very weak swelling visible inside aperture. Colour pale yellow-brown with 2 indistinct orange-brown bands, one in middle of whorls, the other just adapical to periphery/suture; abapical half of base and corresponding portion of inner lip orange-brown. One specimen has the 2 orange bands fused into a single broad, rather distinct band.

Dimensions

| | Height | Diameter |
|---|---|---|
| Holotype | 0.90 mm | 0.50 mm |
| Paratype | 0.90 mm | 0.51 mm |

*Operculum.* Typical of genus (fig. 15h).

*Radula.* Absent.

Operculum examined from W. side of Carnac Is., W.A. (SEM stub no. 491).

TYPES. Holotype (C. 106473) and 4 paratypes (C. 106474), AM; 1 paratype (WAM 299-79), WAM.

TYPE LOCALITY. Quininup, S.W.A., 1972, coll. J. Hewitt.

ADDITIONAL MATERIAL EXAMINED. *W.A.*: S.W. end of Garden Is., off Fremantle (1). Garden Is. (2). Bathurst Pt., Rottnest Is. (4).

DISTRIBUTION AND HABITAT. Known only from the vicinity of Perth and Rottnest Island, Western Australia, the single living specimen obtained on sublittoral algae (fig. 22).

REMARKS. The shell of this species suggests a tall-spired *Eatoniella* in its shape and, in particular, the 2 weak indentations in the outer lip. The operculum is, however, typical of *Tubbreva* and no trace of a radula was found in the one specimen available with soft parts.

### **Tubbreva parva** sp. nov.

Figs 4j; 15i.

Derivation of name: *parva* (Latin) = minute.

DESCRIPTION. *Shell.* Minute, conical to elongately conical, smooth, shining, translucent, nonumbilicate, pale orange. Protoconch of 1½ smooth whorls; teleoconch of up to 4 (usually 3) slightly convex whorls, smooth except for weak axial growth lines. Aperture subquadrate; inner lip thin, columella with weak bulge; outer lip thin and simple. Colour uniform pale orange to yellowish-orange, inner lip slightly darker than rest of shell.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 0.91 mm | 0.55 mm |

| | | |
|---|---|---|
| Paratype | 0.90 mm | 0.60 mm |

*Operculum*. Typical of genus (fig. 15i).

*Radula*. Absent.

Operculum examined from type locality (SEM stub no. 458).

TYPES. Holotype (C. 106221) and 3 paratypes (C. 106222), 1 paratype (C. 106223), AM; 1 paratype (MO 6317), QM; a shell and 1 operculum (SEM stub no. 458).

TYPE LOCALITY. S. side of Caloundra Head, Caloundra, Qld, on algae (C. 106221, C. 106222) and on coralline algae (C.106223), semi-exposed rock platform, mid-tide pool, low tide, 20 Oct. 1976, coll. I. Loch and B. Duckworth.

ADDITIONAL MATERIAL EXAMINED. *Qld*: Off Flat Rock, North Stradbroke Is., Moreton Bay, 24-30 m (2).

DISTRIBUTION AND HABITAT. Caloundra to North Stradbroke Is., southern Queensland, living on littoral and sublittoral algae on exposed coasts (fig. 22).

REMARKS. This species differs from the preceding one by its simple outer lip and uniform orange colour.

### Genus **Pseudopisinna** nov.

Type species: *Estea gregaria* Laseron, 1950.

DIAGNOSIS. Shell minute, pupoid nonumbilicate, smooth or with axial ribs and a subsutural groove. Protoconch smooth, simple, dome-shaped, paucispiral. Aperture circular, simple, inner lip uniformly broad, its edge convex, outer lip not sinuate. Operculum transparent, rather thin, with no internal ridge and with straight, simple peg projecting beyond margin. Radula with minute, simple central teeth; lateral teeth broadly ∩-shaped with few weak cusps; inner marginal teeth long, with 1-2 large, spade-like cusps and thickened in proximal half; outer marginal teeth very short, with 2 widely divergent, sharp cusps. Animal with head-foot typical of family.

DISTRIBUTION. Australia, Papua New Guinea and New Caledonia.

REMARKS. The genus name is based on the remarkable similarity in the shell characters between species of this genus and species of the rissoid genus *Pisinna* Monterosato (see Ponder & Yoo, 1976). The smooth protoconch of *Pseudopisinna* species is about the only reliable shell character separating *Pseudopisinna* from *Pisinna* species, which have a protoconch sculpture of rows of minute punctures, but the opercular, radular and head-foot characters are very different.

*Pseudopisinna* differs from other genera in the Cingulopsidae in the rudimentary central teeth of the radula and the ∩-shaped lateral teeth, as well as the circular aperture with its wide, simple inner lip. It is also the only cingulopsid genus to exhibit strong axial ribbing amongst the species it encompasses. The unusual radula can be derived from a more 'normal' cingulopsid radula by reduction of the central teeth and the lengthening of the inner edge of the lateral teeth, a trend commenced in two subgenera of *Eatoniopsis (Rufodardanula* and *Pilitonia)*. The marginal teeth are not greatly dissimilar from those of *Eatonina*, although the bases of the inner marginal teeth have become considerably thickened and no longer serve to support the very small outer marginal teeth as they do in *Eatonina*.

## KEY TO THE AUSTRALIAN AND TROPICAL INDO-PACIFIC SPECIES OF *PSEUDOPISINNA*.

1. Shell uniform brown ........................................................................ 2
   Shell yellow to white with brown band ............................................... 3
2. Shell less than 1 mm in length, with aperture protruding beyond line of spire, with weak axial ribs ..........................................................*alvea* (Laseron)
   Shell usually greater than 1 mm in length, with aperture in line with spire, smooth or with weak to strong axial ribs ..............................*gregaria* (Laseron)
3. Shell with distinct axial ribs on body whorl ....................................*costata* nov.
   Shell without axial ribs ..........................................................*balteata* nov.

### (?) **Pseudopisinna alvea** (Laseron, 1950)

Fig. 5a

*Estea alvea* Laseron, 1950: 271, fig. 45.

DESCRIPTION. *Shell.* Minute, elongate pupoid, yellowish-brown (faded), aperture protruding beyond line of spire, sculptured with weak, close, prosocline axial riblets. Protoconch of nearly 1½ apparently smooth whorls; teleoconch of very lightly convex whorls; spire outline convex over the first two whorls, almost parallel-sided over the following two. Aperture large, circular, inner lip broad, somewhat separated from base abaxially, outer lip slightly thickened behind edge, a very weak varix externally.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 0.92 mm | 0.48 mm |

Operculum and Radula. Unknown.

TYPES. Holotype (C. 106224), AM.

TYPE LOCALITY. Sow and Pigs Reef, Sydney Harbour, N.S.W., 11-16 m.

DISTRIBUTION AND HABITAT. Known only from the type locality and has not been collected alive (fig. 24).

REMARKS. The holotype is the only specimen of this species available to us. It is similar to *Pisinna oblata* (Laseron, 1956) (see Ponder & Yoo, 1976) but is much smaller than that species or any other known species of *Pisinna*. The "dead", faded and rather worn shell cannot be placed in either *Pissinna* or *Pseudopisinna* with certainty, but we have tentatively included this species in *Pseudopisinna* mainly on the basis of its minute size and general similarity to *P. gregaria;* however, the protruding aperture and thickened outer lip are more typical of *Pisinna* species.

### **Pseudopisinna balteata** sp. nov.

Figs 5b; 16a-g

Derivation of name: *balteatus* (Latin) = girdled.

DESCRIPTION. *Shell.* Minute, ovate-conical to broadly pupoid, smooth, translucent white with a narrow peripheral brown band. Protoconch dome-shaped, of 1½ smooth whorls; teleoconch of 2½ weakly convex whorls, spire outline convex. Aperture relatively large, circular, inner lip broad, separated from base abapically; outer lip simple. Surface smooth except for weak growth lines and an inconspicuous narrow spiral depression abapical to sutures. Colour translucent dirty yellowish-white to white, with a narrow peripheral brown band also visible adapical to sutures on spire whorls.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 0.94 mm | 0.57 mm |
| Paratype | 0.86 mm | 0.52 mm |
| Figured specimens | | |
| Paratype (SEM stub no. 427) | 0.84 mm | 0.51 mm |
| Port Moresby, P.N.G. (SEM stub no. 133) | 0.86 mm | 0.53 mm |
| Nouméa, New Caledonia (SEM stub no. 261) | 0.92 mm | 0.58 mm |

*Operculum.* Typical of genus (figs 16d-f).

*Radula.* Identical to that of the Western Australian form of *P. gregaria gregaria* and of *P. gregaria rugifera* (see below) (fig. 16g).

Opercula and radulae examined from type locality (SEM stub no. 427), Port Moresby, Papua New Guinea (SEM stub no. 133) and off Nouméa, New Caledonia (SEM stub no. 261).

TYPES. Holotype (C. 106228) and many paratypes/24w (C. 106229), AM; 5 paratypes (MO 6319), QM; 1 shell, 2 opercula and 1 radula (SEM stub no. 427).

TYPE LOCALITY. Yam Is., Torres Strait, Qld, reef edge on S. side, on *Sargassum*, 6 July 1976, coll. W. F. Ponder and I. Loch.

ADDITIONAL MATERIAL EXAMINED. *Papua New Guinea:* Basilisk Passage, Port Moresby, 2 m, on algae on reef (8/3w). *New Caledonia:* Récif Bay, Poum, 1-4 m, on algae in dead coral in mud and sandy bottom (1). Baie de Radio État, Magenta, Nouméa, on and under stones with some algae and coral, semi-sheltered (1). Croissant Reef, Nouméa, 0-1 m, rock and algae washings on exposed sandy flat with some coral rubble and algae (11/5w). W. side of Île Signal, Nouméa, 0-2 m, on algae, on sandy and dead coral bottom (33/18w). W. end of Ricaudy Reef, Nouméa, 0-1 m, rock and weed (ANSP 271089) (16). 6.4 km N.W. of Gatope Is., off Voh, 1-4 m, sand, weed and rubble, inner edge of barrier reef (ANSP 269517) (2). *Qld:* Four Mile Reef, Port Douglas, in debris from outer reef, extreme low tide (2). Off Cairns (2).

DISTRIBUTION AND HABITAT. North Queensland, Papua New Guinea and New Caledonia on algae and debris on the lower littoral and shallow sublittoral (fig. 24).

REMARKS. The white shell with the narrow brown peripheral band and the absence of axial ribs are the features which readily distinguish this species from its congeners. It is probably more widely distributed in the tropical Indo-Pacific than indicated by the available material.

### **Pseudopisinna costata** sp. nov.

Figs 5c; 16h-j.

Derivation: *costatus* (Latin) = ribbed.

DESCRIPTION. *Shell.* Minute, pupoid, yellowish-white with a brown sutural band and base, with axial riblets and a row of nodules abapical to suture. Protoconch of 1½ smooth whorls; teleoconch of 3 lightly convex whorls. Aperture circular, inner lip broad, abapical portion thickened and well separated from base. Axial ribs prominent on last 1½ whorls, prosocline, extending on to base, cut off abapical to suture by a narrow, rather deep groove to form a row of nodules. Colour yellowish-white, protoconch pale brown, base and a narrow band abapical to suture orange-brown.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 0.98 mm | 0.50 mm |
| Paratype | 0.92 mm | 0.50 mm |

*Operculum.* Typical of genus (fig. 16i).

*Radula.* Almost identical to that of *P. gregaria rugifera,* the Western Australian form of *P. gregaria gregaria* (see below) and *P. balteata* (see above) but with only a single inconspicuous protuberance on the thickened proximal part of the inner marginal teeth (fig. 16j).

Operculum and radula examined from type locality (SEM stub no. 174).

TYPES. Holotype (C. 106230) and 3/4 w paratypes (C. 106231), AM; 1 paratype (WAM1501-78), WAM; 1 shell, 2 opercula and 2 radulae (SEM stub no. 174).

TYPE LOCALITY. Houtman Abrolhos, W.A., on red algae, 6 m, Mar. 1970, coll. H. Klynsmith, pres. S. White.

ADDITIONAL MATERIAL EXAMINED. *S.W.A.*: Quininup (5). *W.A.:* S.W. end of Garden Is., off Fremantle (2). Garden Is. (3)

DISTRIBUTION AND HABITAT. South Western Australia to Perth area and Houtman Abrolhos, known living only on sublittoral algae (fig. 24).

REMARKS. This species is similar to the extreme Western Australian forms of *Pseudopisinna gregaria* in shape but is smaller and has a different colour pattern and heavier axial ribs. *P. gregaria rugifera* has similar sculpture but it is on all whorls of the teleoconch, is rather broader and a little larger, and has a different colour, being uniformly brown.

### **Pseudopisinna gregaria gregaria** (Laseron, 1950)

Figs 5d,e; 17a-i

*Estea gregaria* Laseron, 1950: 271, fig. 44.

DESCRIPTION. *Shell.* Minute, broadly to narrowly pupoid, solid, dark brown to orange brown. Protoconch of 1½ dome-shaped, smooth whorls; teleoconch of about 2½ weakly convex whorls, spire outline lightly convex. Aperture circular, with broad inner lip well separated from base abapically. Surface smooth or with weak axial ribs separated from a row of nodules immediately abapical to suture by a weak groove. Intermediate forms have only a groove or a groove and a row of nodules. Colour dark orange-brown to red-brown, often translucent-yellowish behind outer lip.

Dimensions

| | Length | Diameter |
|---|---|---|
| Lectotype | 1.13 mm | 0.64 mm |
| Paralectotype | 1.12 mm | 0.62 mm |
| Figured specimens | | |
| Forster, N.S.W. (SEM stub no. 172) | 1.02 mm | 0.60 mm |
| Collaroy, Sydney, NSW | 1.06 mm | 0.61 mm |
| Yallingup, S.W.A. (SEM stub no. 131) | 1.13 mm | 0.64 mm |

*Operculum.* Typical of genus (figs 17d, e, g).

*Radula.* Typical of genus; central teeth minute, simple. Lateral teeth with a broad but weak cusp at apex of arch and a cusp-like projection on inside extension. Inner marginal teeth with 3-4 cusps at distal end, outermost short and sharp, next largest, longest and blunt, inner 1-2 sharper; proximal half of teeth thickened, with 2-3 cusp-like projections. Outer marginal teeth small with two sharp "cusps", one directed inwards, the other downwards (figs 17b, c, h, i).

Opercula and radulae examined from Forster, N.S.W. (SEM stub no. 172), Jervis Bay, N.S.W. (SEM stub no. 333), Yallingup, S.W.A (SEM stub no. 131) and Cape Naturaliste, S.W.A. (SEM stub no. 332).

*Head-foot.* Tentacles rather long, constantly lashing up and down, eyes in small bulges at their outer bases, snout short, bilobed. Foot with bluntly rounded anterior end, posterior end sharply rounded; posterior mucous slit conspicuous, about two thirds length of foot. Colour semitransparent white. (Observed from North Harbour, Sydney, N.S.W. and Eaglehawk Neck, Tasmania).

TYPES. Lectotype (C. 105676) (here chosen) and 21 paralectotypes (C. 105677), AM.

TYPE LOCALITY. North Harbour, Sydney, N.S.W., alive under stones.

ADDITIONAL MATERIAL EXAMINED. *Qld*: Off Flat Rock, North Stradbroke Is., 24-30 m, on algae (1). *N.S.W.*: Woolgoolga (1). S.W. of Solitary Is., 15 m (1). Off Crowdy Head, 91 m (3). Forster, on green algae, low tide, open coast (1). Port Stephens (12). Off Port Stephens, 64 m (1). 3.2 km E. of Nelsons Bay, Port Stephens, on algae, moderately exposed rocks (5w). Off Broughton Is., near Port Stephens, 46 m (1). Collaroy Beach, Sydney (4). N. side Long Reef, Collaroy, on coralline algae, semi-exposed platform, low tide (7). N.E. side Long Reef, on coralline algae in pool, low tide (many). S. side Long Reef, on short brown algae (3). Long Reef, under rocks (1); on short brown algae, outer point (3w). Ocean beach, Manly, Sydney (3). North Harbour, Sydney, dredged (2). Forty Baskets Beach, North Harbour (2). Fairlight, North Harbour, on mixed short algae (4); under stones (1). Near Fairlight Pool, on coralline algae (9). S.E. side of Reef Bay, North Harbour (6). Chinamans Beach, Middle Harbour, 5 m (9). Wyargine Pt., Middle Harbour, on algae (10). Middle Harbour (4). Middle Head (many). Off Sow and Pigs Reef, Sydney Harbour, 11-16 m (21). E. side of Sow and Pigs Reef, 3.6 m (6). Bottle and Glass Rocks, Sydney Harbour, 9 m (4). 5 km E. of Long Pt., Malabar, Sydney, 39 m (2). Ocean beach, Kurnell, Botany Bay (1). Gunnamatta Bay, Port Hacking (1). Shell Harbour, on algae (1). Honeymoon Beach, Jervis Bay, on short turf, red and brown algae, low tide (13). S. side of Ulladulla, on small brown algae, sheltered reef, outside breakwater (8). On seaward side of long rocky point, Batehaven, Batemans Bay, on red algae, medium exposure (many). Wimbie Beach, Batemans Bay, on fairly exposed rocks, on coralline algae (many); under stones (9). Bermagui (19). Twofold Bay, Eden, on coralline algae (13). Bitangabee, N. side of Green Cape, on coralline algae, in sheltered pool (12); under stones medium exposure (2). Green Cape, Disaster Bay side, 15 m (1). *Tasm.* Murray Pass., Deal Is., Bass Strait, 30-50 m, on algae (many/many wet). East Cove, Deal Is., 6-15 m (13/40w). Little Squally Cove, Deal Is., 10-30 m, on algae (many/many wet). Deal Is., 6 m, on algae (9). S. of Cape Lodi, 28 m (6). Pirates Bay, Eaglehawk Neck, on brown algae, on intertidal rocks (25/7w); under stones (9). Eaglehawk Neck (23). Primrose Pt., Frederick Henry Bay., on matted green algae, low tide (1); on matted algae (16/22w); on coralline algae (11); low tide (9). *Vic.:* E.S.E. side Gabo Is., 21 m, on red algae (11); 15-18 m, on algae and detritus (6). S.S.E. side Gabo Is., 28 m, on red algae (28). Between Eagle and Crawfish Rock, Western Port, 3-6 m (8). Portarlington, Port Phillip Bay, mixed coralline, brown algae and *Caulerpa,* low tide (48). *S.A.:* 3 km S. of Normanville, on rock-strewn platform, medium exposure (2). Tumby Bay (3). Pearson Is., Investigator Group, 18 m on algae (3). *S.W.A.:* Mississippi

Bay., 48 km E. Esperance, 0-2 m, on algae, sheltered side of W. head of bay (1). Hopetoun Jetty, 0-2 m, on algae, semi exposed-semi sheltered reef (3), South Pt., S. of Two Peoples Bay, near Albany, 0-2 m, on algae in large sheltered pool, outer coast, low tide (2). Kilcarnup, N. side of Margaret River (3). Quininup (5). Yallingup,on algae, on limestone platform (many/many wet). N. side Cape Naturaliste lighthouse, under stones, low tide (many/many wet). Cape Naturaliste (2). Bunker Bay, 11 km W. of Dunsborough, 1-3 m, on short algae, semi-sheltered (8). Dunsborough, on short algae and coralline algae, low tide (42); 1-2 m, *Cymadocea* washings (5/3w). 4-8 km off Peppermint Grove, between Bunbury and Busselton, 4-8 m (31). *W.A.:* S. side Pt. Peron, S. of Fremantle, on algae and *Posidonia*, sheltered (5). Pt. Peron, 2-3 m (9); 0-4 m, sheltered side, on *Posidonia* and algae (9). S.W. side Pt. Peron, 3.5 m, on algae, exposed (many). S.W. end of Garden Is., off Fremantle (30); 0-3 m, on algae (30/15w). Garden Is. (24). W. side Carnac Is., on rubble, low tide (8); 4-8 m, on algae (many/2w). Woodmans Pt., S. of Fremantle, on coralline algae, low tide (11); on *Caulerpa* (4/7w); under stones (2); on algae, 1-3 m (21w). W. end Salmon Bay, Rottnest Is., *Lithothamnion* washings from reef edge (5). W. end reef, Rottnest Is., *Lithothamnion* washings from intertidal reef edge (6). Eagle Bay, Rottnest Is., *Lithothamnion* washings from reef edge (2). W. end Thomson Bay, Rottnest Is., 0-2 m, on coralline algae (many); on mixed algae (many). North Pt., Rottnest Is., on coralline algae, protected reef (many/22w). Triggs, Perth, 0-2 m, *Caulerpa* washings on platform, open coast (20); on coralline algae, on platform, open coast (many/20w). Cottesloe Beach, Perth, 0.5 m, on calcareous algae (20/3w). Cottesloe Reef, Perth, on algae (6).

FOSSIL RECORD. Upper Pliocene; Cameron Inlet Formation — Hills Dam at foot of Dutchman (E. side), Flinders Is., Bass Strait (NMV).

DISTRIBUTION AND HABITAT. North Stradbroke Is., southern Queensland to Tasmania and the south coast of Australia and Western Australia to Perth area (including Rottnest Is.), common on algae in the littoral and sublittoral (fig. 24).

REMARKS. This species shows considerable geographic and intrapopulation variation. Typical forms which have broadly pupoid, almost smooth to very weakly axially costate shells (figs 5d, 17a) are the predominant form encountered in N.S.W. The southern coast and Tasmanian populations have similar shells which generally tend to develop a row of weak nodules abapical to the suture and many specimens are slightly more elongately pupoid than the normal N.S.W. form. Western Australian specimens often develop rather distinct axial riblets and have a conspicuous row of nodules abapical to the suture (fig. 17f). There appears to be a complete, probably clinal, gradation between these forms.

The radulae of the N.S.W. and Western Australian specimens examined differ in the Western Australian specimens having 3 (not 2) more prominent projections on the basal part of the inner marginal teeth and 4 (not 2) cusps distally. In view of the virtually continuous distribution of this species around the southern coast and the probable clinal nature of the shell variation, the differences in radular structure are here assumed not to be important and may also follow a clinal pattern.

### **Pseudopisinna gregaria rugifera** subsp. nov.

Figs 5f; 17j-l

Derivation of name: *rugiferus* (Latin) = bearing wrinkles.

DESCRIPTION. *Shell.* Minute, pupoid, solid, nonumbilicate, dark brown with strong axial ribbing. Protoconch of 1½ whorls; teleoconch of 3¼ very weakly convex whorls, sculptured with prosocline, closely spaced axial ribs; rather weak and indistinct in a few specimens but well-developed in most. A narrow, usually distinct groove abapical to suture with a row of nodules corresponding to ribs between groove and suture; axials often weakly nodular immediately abapical to groove; base smooth except for growth lines; axials weak on last ¼ of body-whorl. Aperture circular, inner lip broad, edge convex, separated from base in abapical portion; outer lip weakly prosocline. Suture bent abapically just abapertually to outer lip. Colour dark brown, translucent yellowish-brown on last ⅛ of body whorl, inner lip slightly darker than rest of shell.

Dimensions

| | Length | Diameter |
|---|---|---|
| Holotype | 1.04 mm | 0.58 mm |
| Paratype | 0.98 mm | 0.56 mm |
| Figured specimen | | |
| Heron Is., Qld (SEM stub no. 208) | 0.94 mm | 0.52 mm |

*Operculum.* Typical of genus (fig. 17k).

*Radula.* Identical to that of *P. gregaria gregaria* from Western Australia (see Remarks under *P. gregaria gregaria*) (fig. 17l).

Opercula and radulae examined from S.W. side of Heron Is., Qld (SEM stub no. 208).

*Head-foot.* As in *P. gregaria gregaria.*

TYPES. Holotype (C. 106225) and many paratypes (C. 106226 and C. 106227), AM; 5 paratypes (MO 6318), QM.

TYPE LOCALITY. S. side of Heron Is., Qld, opposite research station, in coral rubble with algal coating, 2-8 m, 27 Dec. 1976, coll. W. F. Ponder.

ADDITIONAL MATERIAL EXAMINED. *New Caledonia*: 6 km N.W. of Gatope Is., off Voh, 2-4 m, amongst sand, weed and rubble on inner edge of barrier reef (ANSP 269517) (2). *Qld:* Heron Is. (9); N. side, in coral rubble, in outer part of lagoon (18/22w); 3 km E. of Is., in lagoon, on weed, on coral 'bommie' (1); off S.E. side, 6 m (1); S.W. side, in coral rubble behind reef crest (many/many wet); on red algae, outer reef crest on S.W. side (5). Off Moreton Bay, 75-80 m (1).

DISTRIBUTION AND HABITAT. Heron Island, Capricorn Group, Great Barrier Reef, Queensland and New Caledonia, on algae and rubble, lower littoral and sublittoral (fig. 24).

REMARKS. This subspecies does not differ greatly from the Western Australian form of *P. gregaria gregaria* except that the axial costae are more strongly and regularly developed. Because no record of *P. gregaria gregaria* is known north of North Stradbroke Island on the east coast of Australia despite suitable habitat being sampled fairly extensively, it is assumed that there is a real break in the distribution of *P. gregaria* resulting in the effective isolation of a subspecies apparently restricted to the southern Barrier Reef and New Caledonia. There are no records of *P. gregaria* along the northern coast or north Queensland but the similarity of the shell and radula of the Queensland subspecies to the Western Australian form of *gregaria* suggest that the present distribution of *P. gregaria rugifera* may be a relic of a previously continuous tropical Australian distribution.

A single damaged specimen dredged off Moreton Bay is tentatively referred to this subspecies. The shell is pale and may be a Pleistocene fossil.

## ACKNOWLEDGEMENTS

This work was supported to a large extent by an Australian Research Grants Committee grant (H70/17338). SEM facilities were provided at the Electron Microscope Unit at the University of Sydney and we gratefully acknowledge the assistance given by the personnel at the Unit. The examination of overseas type material was made possible by financial support received by one of us (W.F.P.) from the Australian Research Grants Committee, The Science and Industry Endowment Fund, the British Council, the Ian Potter Foundation and the Australian Museum Trust.

We gratefully acknowledge the help that numerous individuals and institutions have given us in providing samples and comparative material for use in this and related projects. In particular we would like to thank Dr J. Taylor of the British Museum, Mr W. Zeidler of the South Australian Museum, Mrs S. Slack-Smith of the Western Australian Museum, Dr R. Robertson of the Academy of Natural Sciences of Philadelphia, Dr. H. Rehder formerly of the U.S. National Museum (Natural History) and Dr J. McLean of the Los Angeles County Museum of Natural History.

Dr R. Robertson, Mrs A. Scheltema, Mr P. H. Colman, Mrs J. Kerslake, Dr A. Greer and Mr I. Loch have made valuable comments on the manuscript.

## LIST OF AUSTRALIAN AND TROPICAL INDO-PACIFIC SPECIES OF THE CINGULOPSIDAE

*Eatonina (Eatonina)*

*ardeae* nov., Capricorn Group, Qld.
*capricornea* (Hedley, 1907), Qld.
*colorata* nov., New Hebrides.
*condita* nov., Tasm., Vic., S.A.
*hedleyi* nov., N.S.W.
*heliciformis* nov., New Hebrides, New Caledonia.
*hutchingsae* nov., S. Qld., N.S.W., Tasm., E. Vic.
*lactea* nov., Cook Ids.
*lunata* (Laseron, 1956), Qld, Papua-New Guinea, New Caledonia
*pulicaria pulicaria* (Fischer (in Folin & Périer, 1873)), Mauritius.
*pulicaria pacifica* nov., New Hebrides.
*rubrilabiata* nov., N.S.W.
*sanguinolenta* nov., Tasm., Vic., S.A.
*shirleyae* nov., S.W.A.
*striata* nov., W.A.

*(Coriandria)*
*fulvicolumella* nov., S. N.S.W., Tasm., S.A.
*rubicunda* nov., S.A.

*(Captitonia)*
*lirata* nov., W.A.

*Eatoniopsis (Boogina)*
*voorwindei* nov., N.S.W., N. Tasm.

*(Rufodardanula)*
*castanea* (Laseron, 1950), S.Qld., N.S.W., Tasm., E. Vic.
*porcellana* nov., Capricorn Group, Qld.

*(Pilitonia)*
*translucida* nov., New Hebrides
*westralis* nov., W.A.

*Tubbreva*
  *insignificans* nov., W.A.
  *parva* nov., S. Qld.

*Pseudopisinna*
  (?) *alvea* (Laseron, 1950), N.S.W.
  *balteata* nov., N. Qld, Papua New Guinea, New Caledonia.
  *costata* nov., W.A.
  *gregaria gregaria* (Laseron, 1950), S. Qld, N.S.W., Vic., Tasm., S.A., W.A.
  *gregaria rugifera* nov., Capricorn Group, Qld., New Caledonia.

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Manuscript accepted for publication 22 June, 1978

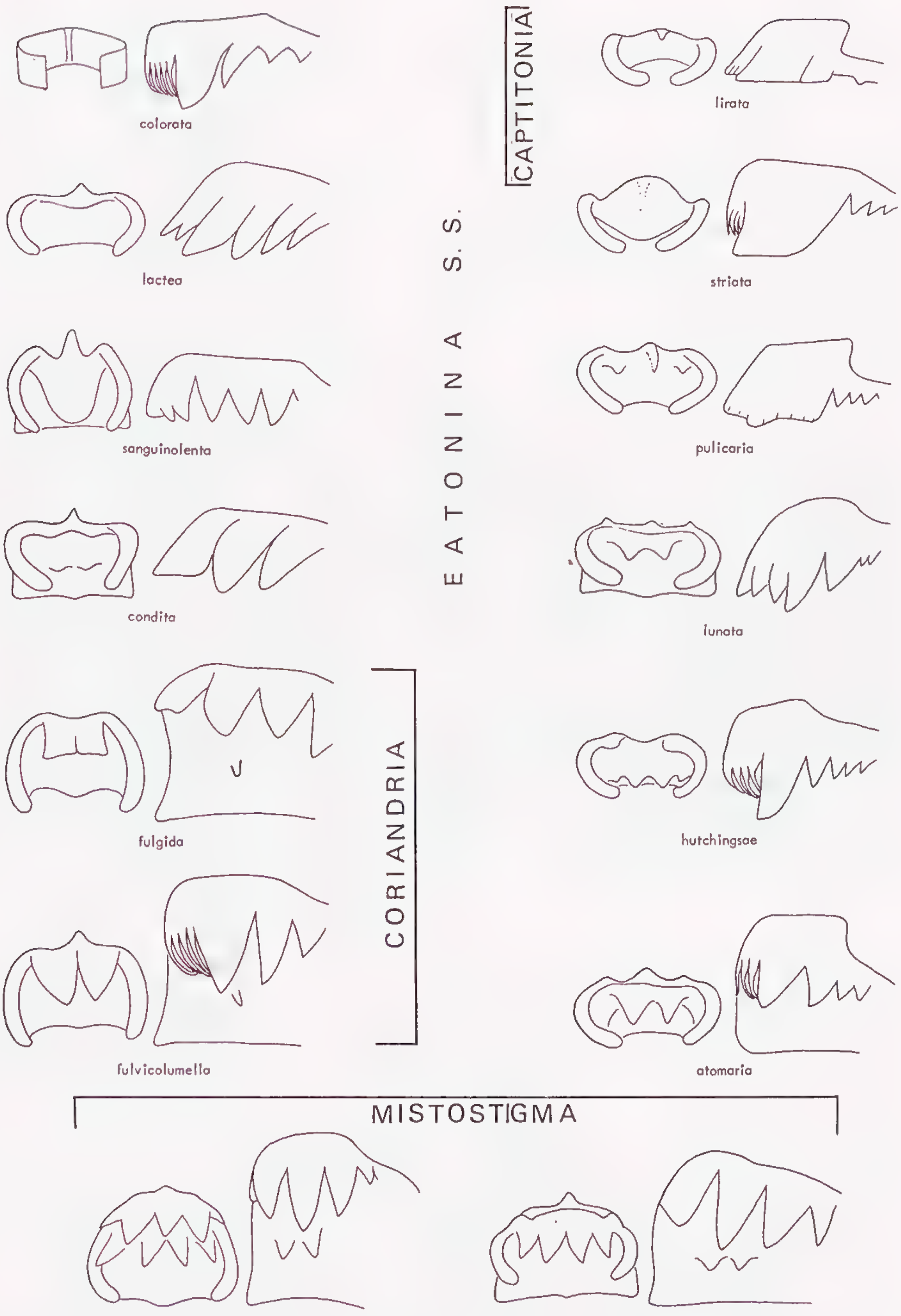

Fig. 1. A diagramatic representation of the relationships of species of *Eatonina* as expressed by radular characters. For further explanation see text.

Fig. 2

a. *Eatonina (Eatonina) capricornea* (Hedley) holotype. Masthead Is., Qld, AM (C. 19354). 1.54 mm x 1.05 mm.
b. *Eatonina (Eatonina) ardeae* sp. nov. holotype. Heron Is., Qld, AM (C. 106169). 1.02 mm x 0.64 mm.
c. *Eatonina (Eatonina) ardeae* sp. nov. (banded specimen) Heron Is., Qld, AM (C. 106191). 1.00 mm x 0.66 mm.
d. *Eatonina (Eatonina) sanguinolenta* sp. nov. holotype. Pt. Sinclair, S.A., AM (C. 106202). 1.46 mm x 0.92 mm.
e. *Eatonina (Eatonina) condita* sp. nov. holotype. Goat Is., near Ulverstone, N. Tasm., AM (C. 107151). 1.30 mm x 0.80 mm.
f. *Eatonina (Eatonina) hutchingsae* sp. nov. holotype. Caloundra, Qld, AM (C. 106175). 1.24 mm x 0.83 mm.
g. *Eatonina (Eatonina) rubrilabiata* sp. nov. holotype. Batehaven, Batemans Bay, N.S.W., AM (C. 106184). 1.33 mm x 0.90 mm.
h. *Eatonina (Eatonina) striata* sp. nov. holotype. Carnac Is., off Fremantle, W.A., AM (C. 106189). 1.08 mm x 0.70 mm.
i. *Eatonina (Eatonina) shirleyae* sp. nov. holotype. Mississippi Bay, E. of Esperance, S.W.A., AM (C. 106187). 1.37 mm x 0.94 mm.

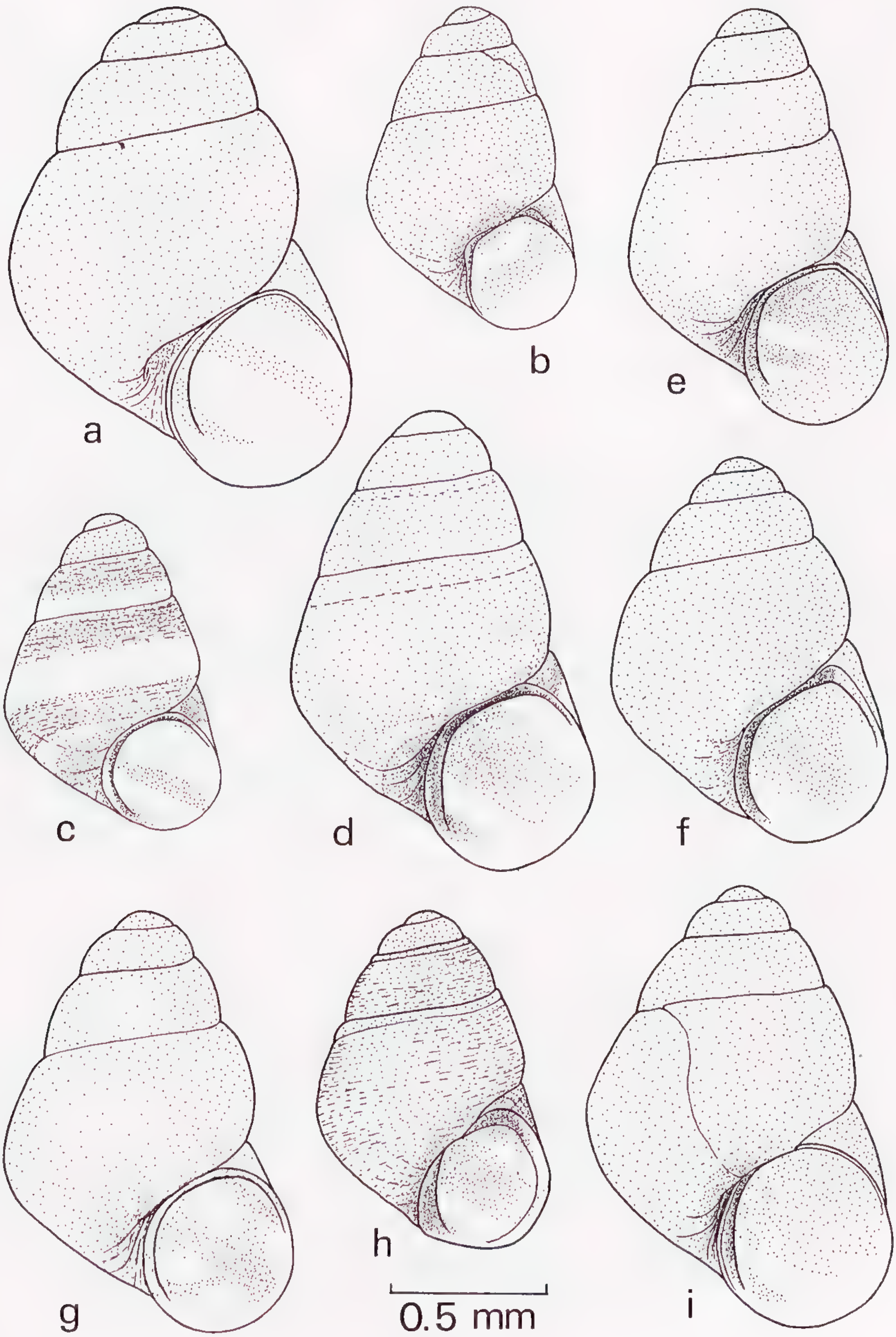
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Fig. 3

- a. *Eatonina (Eatonina) colorata* sp. nov. holotype. Port Vila, Efate, New Hebrides, AM (C. 106193). 0.88 mm x 0.60 mm.
- b. *Eatonina (Eatonina) pulicaria pulicaria* (Fischer) ?paratype. Mauritius, AM (C. 106213). 1.13 mm x 0.78 mm.
- c. *Eatonina (Eatonina) pulicaria pacifica* subsp. nov. holotype. Port Vila, Efate. New Hebrides, AM (C. 106179). 1.20 mm x 0.82 mm.
- d. *Eatonina (Eatonina) heliciformis* sp. nov. holotype. Port Vila, Efate, New Hebrides, AM (C. 106172). 0.95 mm x 0.82 mm.
- e. *Eatonina (Eatonina) hedleyi* sp. nov. holotype. Off Sow and Pigs Reef, Sydney, N.S.W., AM (C. 106267). 0.77 mm x 0.66 mm.
- f. *Eatonina (Eatonina) lactea* sp. nov. holotype. Aitutaki, N. Cook Ids, ANSP (278391). 1.54 mm x 0.84 mm.
- g. *Eatonina (Eatonina) lunata* (Laseron) holotype. Bowen, Qld, AM (C. 105673). 1.86 mm x 1.10 mm.
- h. *Eatonina (Coriandria) fulvicolumella* sp. nov. holotype. South Bruny Is., S. Tasm., AM (C. 106195). 1.15 mm x 0.75 mm.
- i. *Eatonina (Coriandria) rubicunda* sp. nov. holotype. Elliston, S.A., AM (C. 106197). 1.22 mm x 0.83 mm.

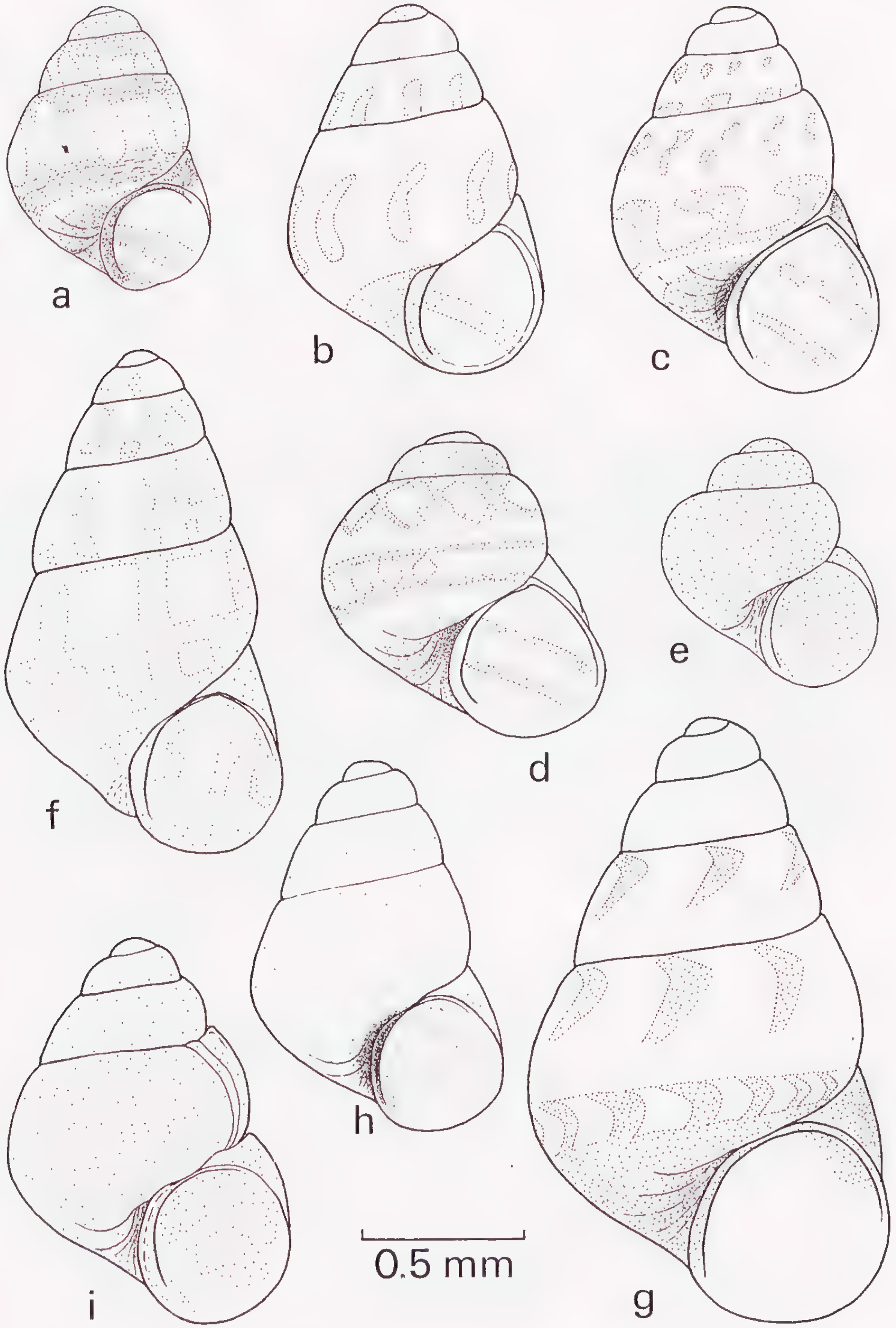
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Fig. 4

a. *Eatonina (Captitonia) lirata* sp. nov. holotype. Garden Is., off Fremantle, W.A., AM (C. 106206). 1.00 mm x 0.64 mm.

b. *Eatoniopsis (Rufodardanula) castanea* (Laseron) lectotype. Middle Harbour, Sydney, N.S.W., AM (C. 105674). 1.30 mm x 0.88 mm.

c. *Eatoniopsis (Rufodardanula) porcellana* sp. nov. holotype. Heron Is., Qld, AM (C. 106209). 1.06 mm x 0.67 mm.

d. *Eatoniopsis (Rufodardanula)* cf. *porcellana* sp. nov. Heron Is., Qld, AM (C. 106212). 0.81 mm x 0.54 mm.

e. *Eatoniopsis (Pilitonia) translucida* sp. nov. holotype. Tanna Is., New Hebrides. AM (C. 106216). 0.60 mm x 0.73 mm.

f. *Eatoniopsis (Pilitonia) westralis* sp. nov. holotype. Mississippi Bay, E. of Esperance, S.W.A., AM (C. 106219). 0.87 mm x 0.90 mm.

g. *Eatoniopsis (Boogina) voorwindei* sp. nov. holotype. Green Cape, N.S.W., AM (C. 106214). 1.56 mm x 1.06 mm.

h,i. *Tubbreva insignificans* sp. nov. holotype. Quininup, S.W.A., AM (C. 106473). 0.90 mm x 0.50 mm.

j. *Tubbreva parva* sp. nov. holotype. Caloundra, Qld, AM (C. 106221). 0.91 mm x 0.55 mm.

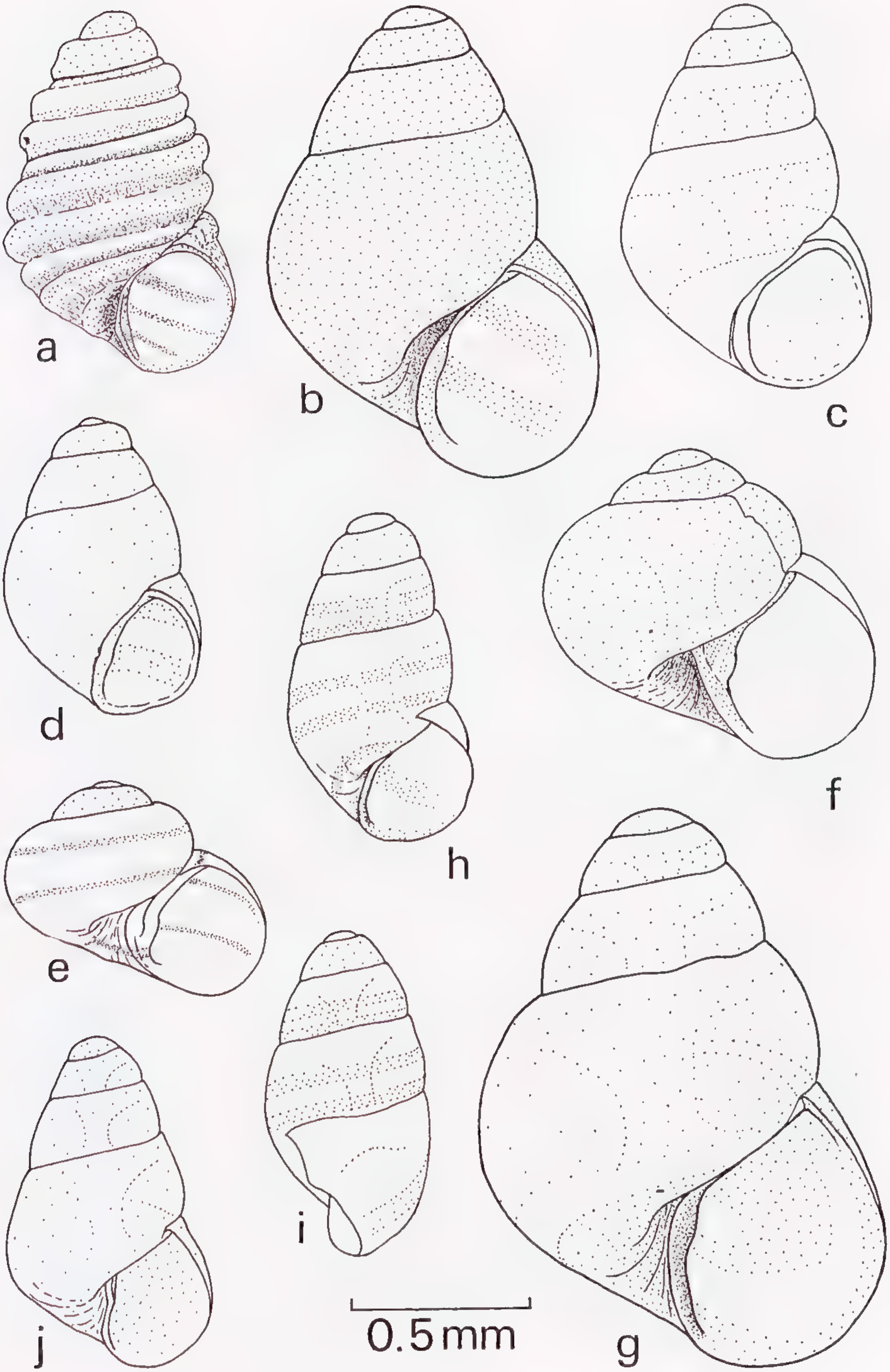
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Fig. 5

a. *(?)Pseudopisinna alvea* (Laseron) holotype. Sow and Pigs Reef, Sydney, N.S.W., AM (C. 106224). 0.92 mm x 0.48 mm.
b. *Pseudopisinna balteata* sp. nov. holotype. Yam Is., Torres Strait, Qld, AM (C. 106228). 0.94 mm x 0.57 mm.
c. *Pseudopisinna costata* sp. nov. holotype. Houtman Abrolhos, W.A., AM (C. 106230). 1.00 mm x 0.50 mm.
d. *Pseudopisinna gregaria gregaria* (Laseron) lectotype. North Harbour, Sydney, N.S.W., AM (C. 105676). 1.13 mm x 0.64 mm.
e. *Pseudopisinna gregaria gregaria* (Laseron) Long Reef, Collaroy, Sydney, N.S.W., AM (C. 108264). 1.06 mm x 0.61 mm.
f. *Pseudopisinna gregaria rugifera* subsp. nov. holotype. Heron Is., Qld, AM (C. 106225). 1.04 mm x 0.58 mm.
g,h. *Eatonina (Eatonina) lunata* (Laseron) head-foot. Palfrey Is. near Lizard Is., Qld.
i. *Eatoniopsis (Rufodardanula) castanea* (Laseron) head-foot. Fairlight, Sydney, N.S.W.
j,k. *Eatonina (Coriandria) cossurae* (Calcara) head-foot. "Tonnara" near San Vito La Capo, W. Sicily, Italy.
l,m. *Eatonina (Coriandria) fulgida* (Alder) head-foot. Wembury, England.

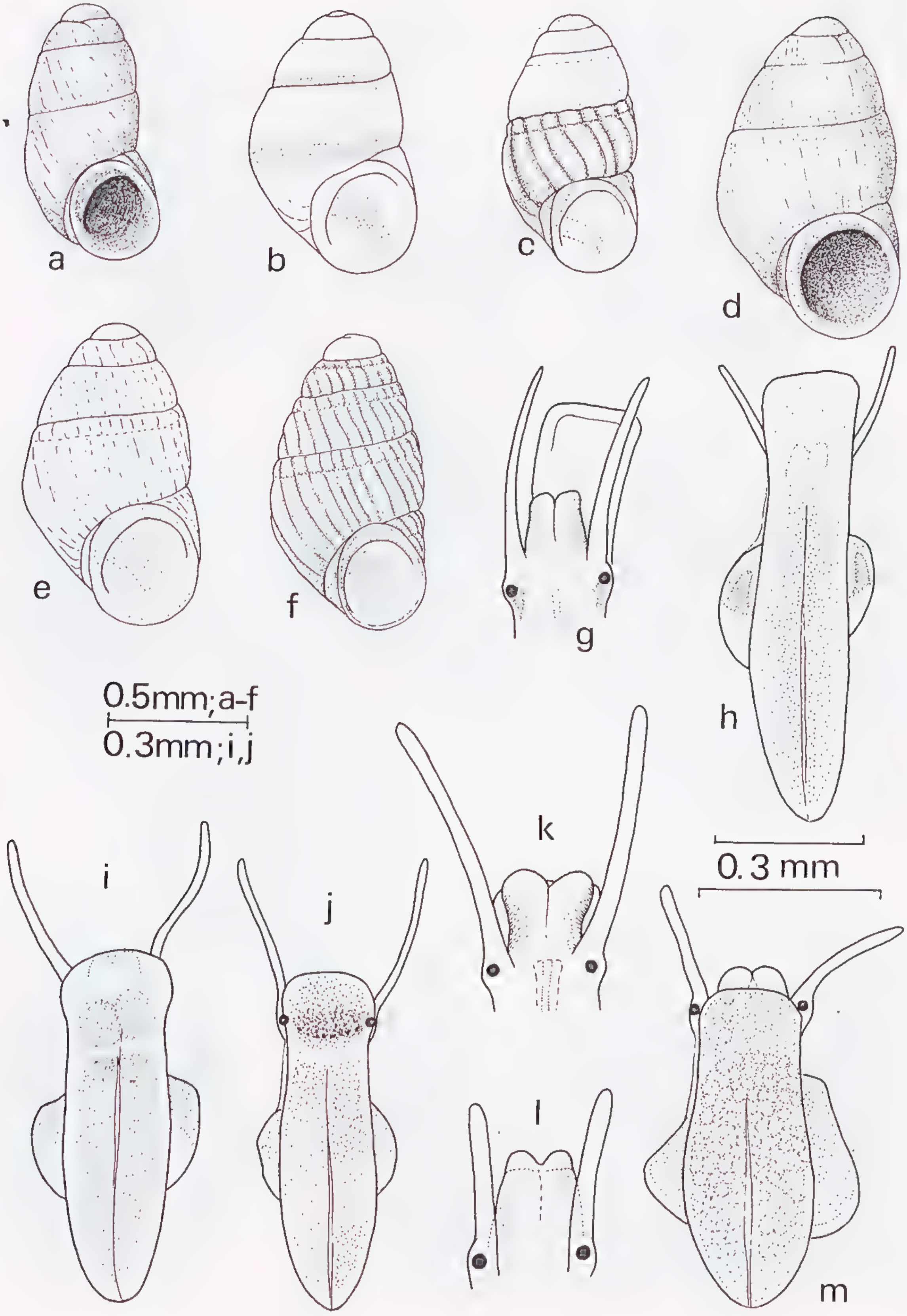
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Fig. 6

*Eatonina (Eatonina) ardeae* sp. nov. **a.** shell — 1.16 mm x 0.73 mm, **b.** shell (banded form) — 1.12 mm x 0.68 mm, **c.** operculum — x 180, **d.** radula — x 1500. S. side of Heron Is., Qld, SEM stub nos 476 (a, c, d) and 490 (b).

*Eatonina (Eatonina) rubrilabiata* sp. nov. **e.** shell — 1.28 mm x 0.83 mm, **f.** operculum — x 170, **g.** radula — x 1700. Batehaven, Batemans Bay, N.S.W., SEM stub nos 459 (operculum), 460 (shell and radula).

*Eatonina (Eatonina) shirleyae* sp. nov. **h.** shell — 1.35 mm x 0.91 mm, **i.** operculum — x 140, **j.** radula — x 1400. Mississippi Bay, E. of Esperance, S.W.A., SEM stub no. 148.

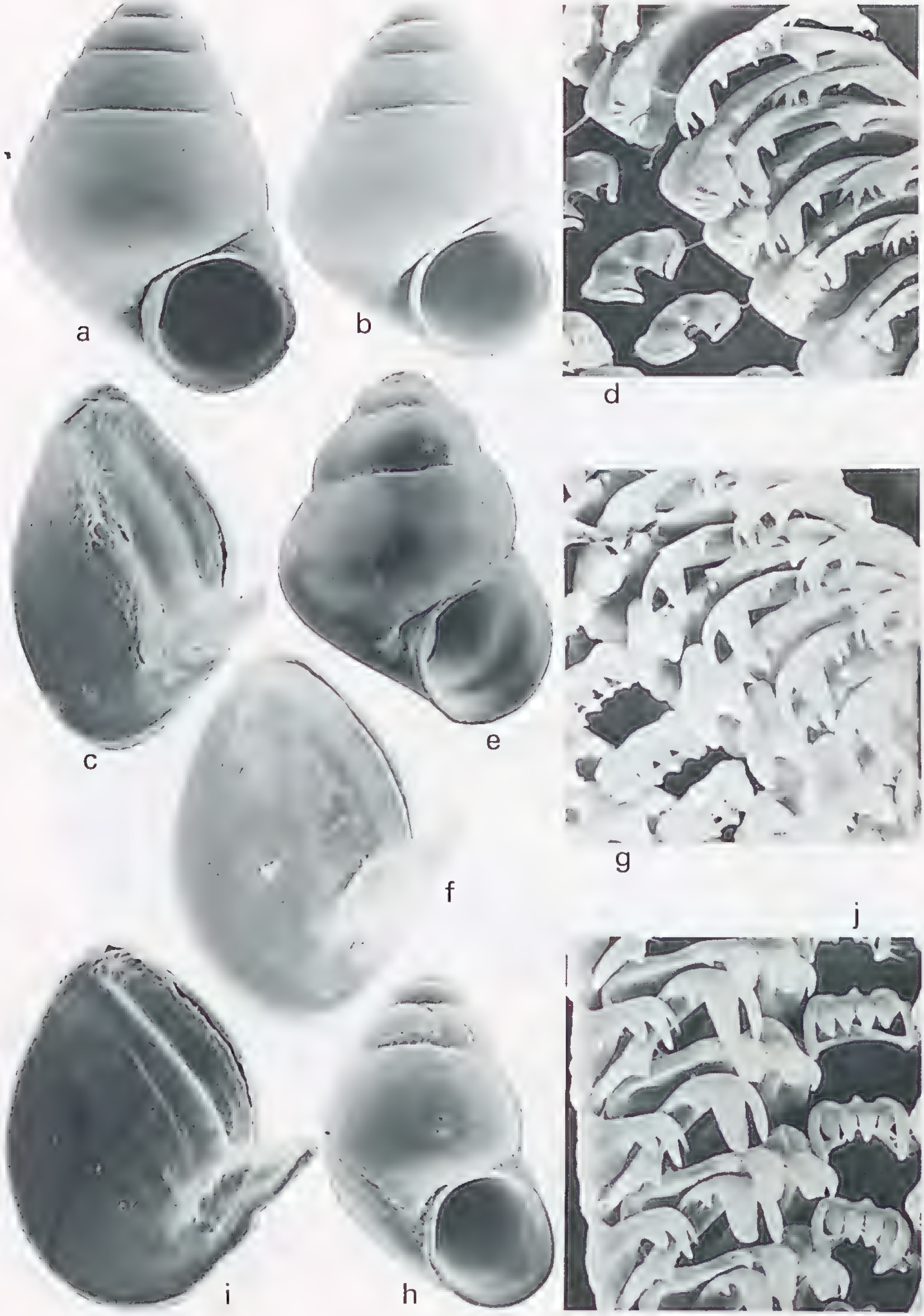
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Fig. 7

*Eatonina (Eatonina) colorata* sp. nov. **a.** shell — 0.90 mm x 0.62 mm, **b & c.** opercula — both x 220, **d.** radula — x 2700, **e.** radula — x 2000. Pt. Ardel, Port Vila, Efate, New Hebrides, SEM stub nos 138 (shell), 479 (opercula, radulae).

*Eatonina (Eatonina) pulicaria pulicaria* (Fischer) **f.** shell — 1.08 mm x 0.68 mm, **g.** operculum — x 160, **h.** radula — x 1200. Arsenal Bay, Mauritius, SEM stub no. 306, **i.** shell — 1.16 mm x 0.70 mm, **j.** radula — x 960. S. side Tombeau Bay, W. Mauritius, SEM stub no. 494, **k.** operculum — x 170. Pt. Fayette, E. Mauritius, SEM stub no. 495.

*Eatonina (Eatonina) pulicaria pacifica* subsp. nov. **l.** shell — 1.30 mm x 0.87 mm, **m.** operculum — x 130, **n.** radula — x 550. Port Vila, Efate, New Hebrides, SEM stub no. 107.

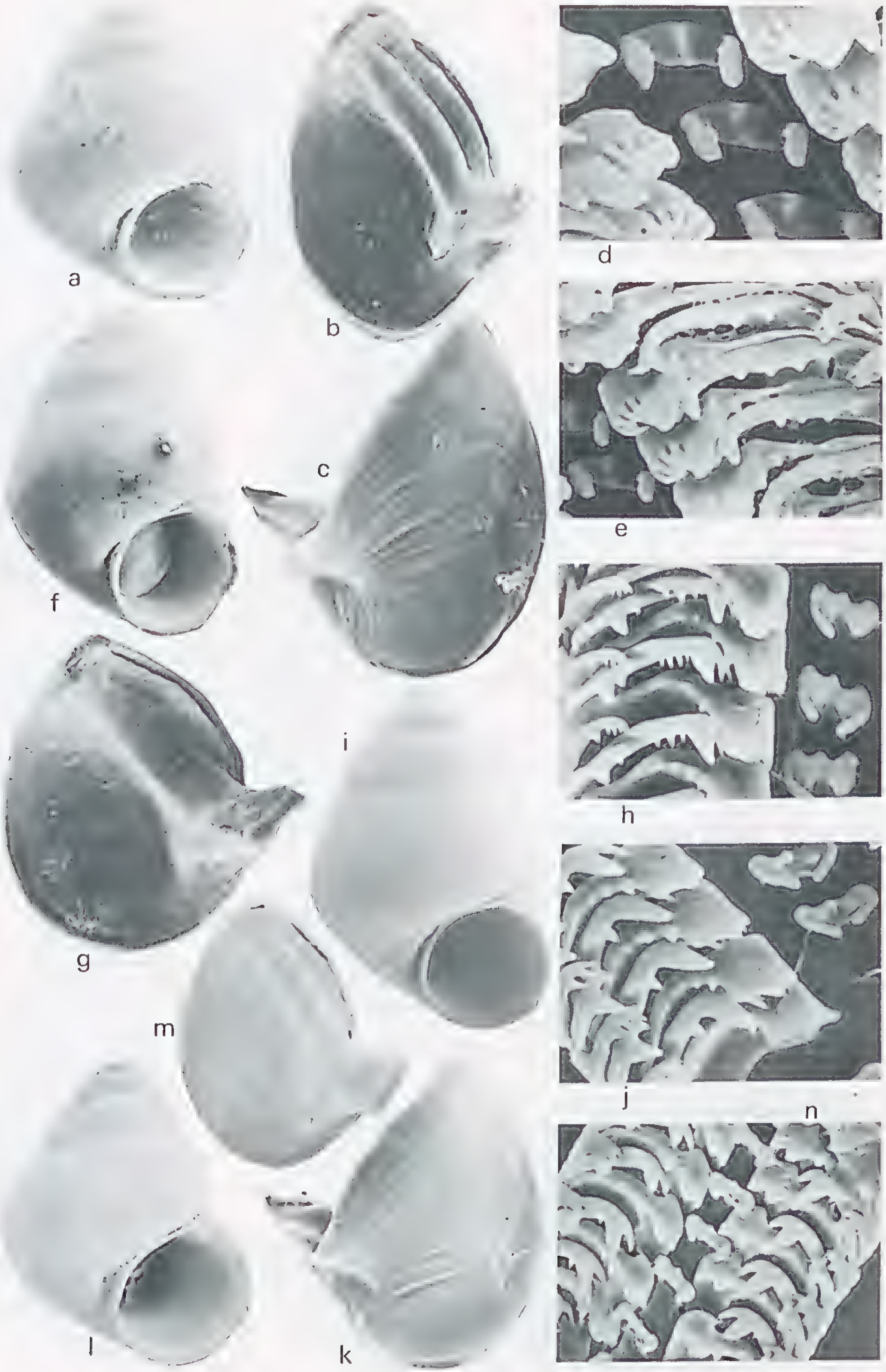
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Fig. 8

*Eatonina (Eatonina) lunata* (Laseron) **a & b.** shells (apertural and side views) — 2.20 mm x 1.18 mm, **e.** radula — x 1200. Lizard Is., Qld, SEM stub nos 157, 167. **c.** shell — 1.48 mm x 0.88 mm, **d.** operculum — x 110. Ile Signal, off Nouméa, New Caledonia, SEM stub no. 140.

*Eatonina (Eatonina) capricornea* (Hedley) **f & g.** shells — **f.** 1.55 mm x 1.00 mm, **g.** 1.44 mm x 0.90 mm, **h.** operculum — x 100, **i.** radula — x 1400, **j.** radula — x 700. Masthead Is., Qld, SEM stub nos 444 (radula), 445 (shells and operculum).

*Eatonina (Eatonina) lactea* sp. nov. **k.** shell — 1.52 mm x 0.80 mm, **l & m.** operculum — both x 150, **n.** radula — x 2200, **o.** radula — x 1400. Aitutaki, N. Cook Ids, SEM stub nos 493 (l., m:, n.), 527 (k, o).

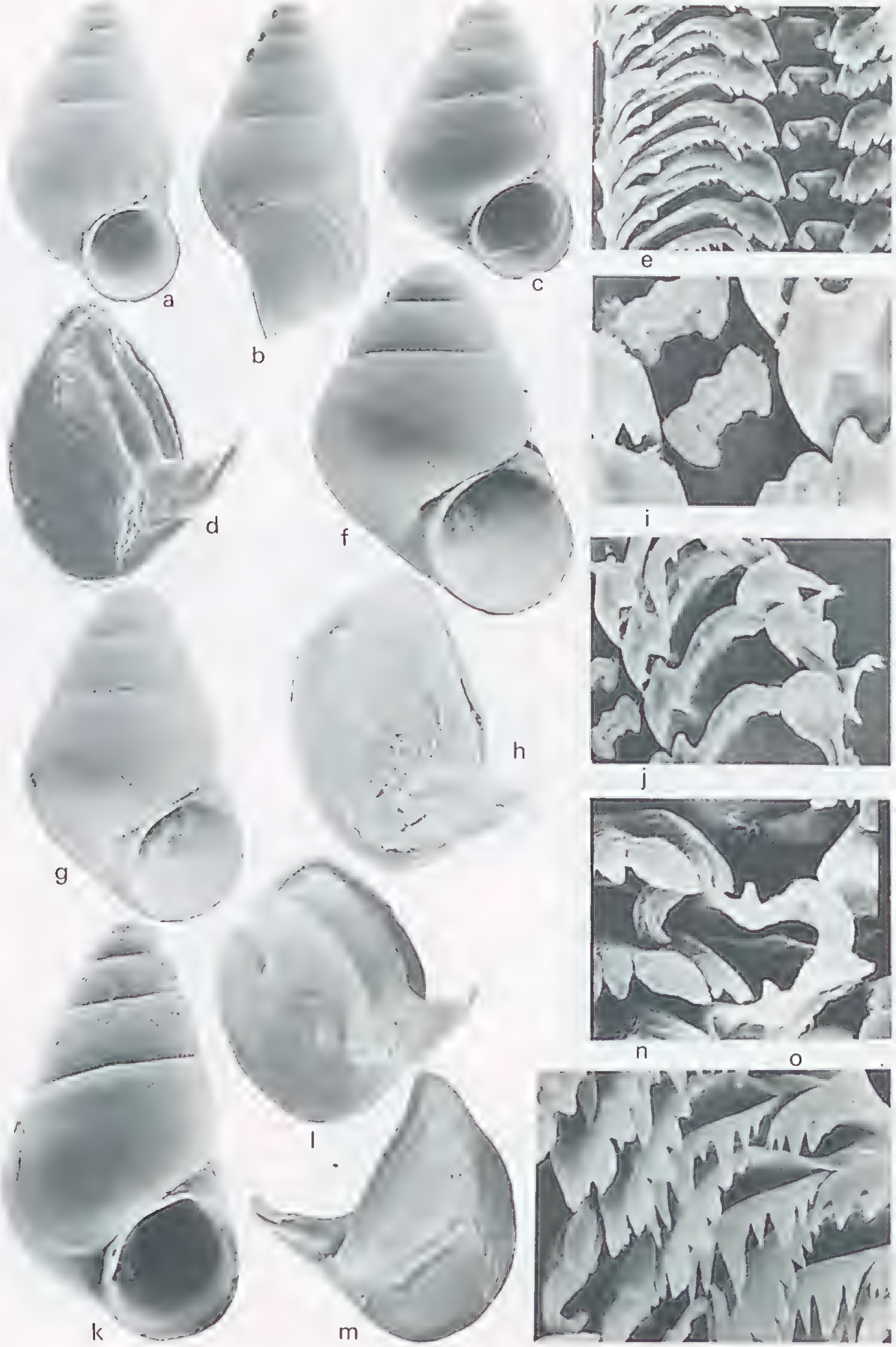
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Fig. 9

*Eatonina (Eatonina) condita* sp. nov. **a.** shell — 1.28 mm x 0.86 mm, **b.** operculum — x 150. Wedge Bay, S. Tasm., SEM stub no. 541. **c** & **d.** shells — **c.** 1.31 mm x 0.83 mm, **d.** 1.30 mm x 0.87 mm, **e.** radula — x 1100. Goat Is., near Ulverstone, N. Tasm., SEM stub nos 425, 542 (shells), 531 (radula). **f.** radula — x 1300. Normanville, S.A., SEM stub no. 438.

*Eatonina (Eatonina) sanguinolenta* sp. nov. **g.** shell — 1.42 mm x 0.90 mm, **h.** operculum — x 120, **i.** radula — x 1500, **j.** radula — x 1300. Pt. Sinclair, S.A., SEM stub nos 329 (shell, operculum), 532 (radula).

*Eatonina (Eatonina) striata* sp. nov. **k.** operculum — x 150, **l.** radula — x 1500. Carnac Is., off Fremantle, W.A., SEM stub no. 473.

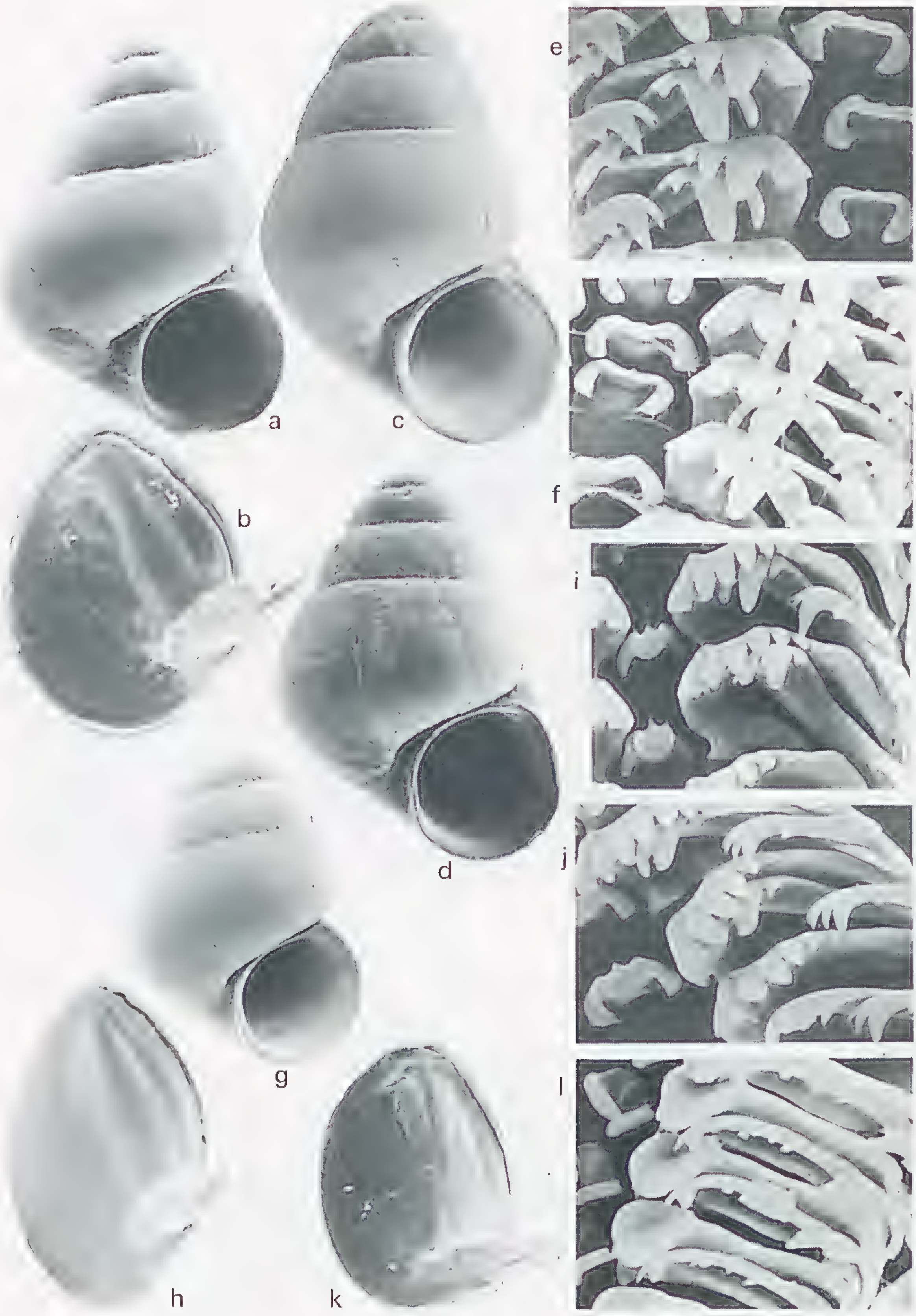
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Fig. 10

*Eatonina (Eatonina) hutchingsae* sp. nov. **a.** shell — 1.14mm x 0.82mm, **b.** radula (central) — x2200, **c.** radula — x1900. Solitary Is., N.S.W., SEM stub no. 437. **d.** shell — 1.28mm x 0.87mm, **e.** operculum — x110, **f.** radula — x1500. Gabo Is., Vic., SEM stub nos 467 (shell, radula), 135 (operculum).
*Eatonina (Eatonina) heliciformis* sp. nov. **g.** shell — 0.96mm x 0.76mm, **h.** operculum — x130. Pt. Ardel, Port Vila, Efate, New Hebrides, SEM stub no. 461. **i.** radula — x1000. Magenta, Nouméa, New Caledonia, SEM stub no. 216.
*Eatonina (Eatonina) hedleyi* sp. nov. **j.** shell — 0.70 mm x 0.66 mm, **k.** operculum — x160, **l.** radula — x1200. Sow and Pigs Reef, Sydney, N.S.W., SEM stub nos 503 (shell & operculum), 487 (radula).

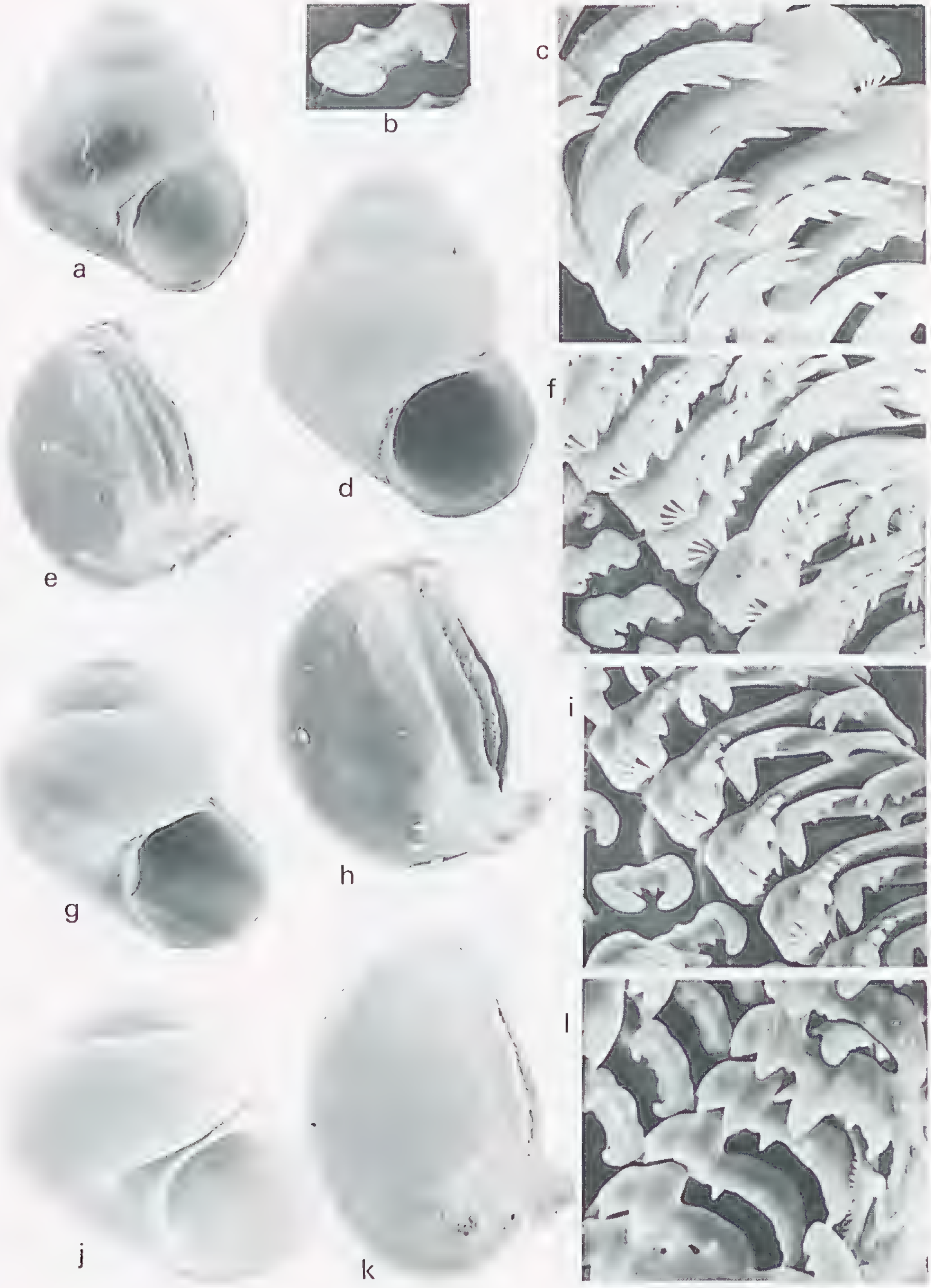
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Fig. 11

*Eatonina (Coriandria) fulvicolumella* sp. nov. **a.** shell — 1.14 mm x 0.76 mm, **b.** operculum — x160, **c.** radula — x1500. Great Taylor Bay, Bruny Is., S. Tasm., SEM stub no. 385. **d.** radula — x1900. Goat Is., near Ulverstone, N. Tasm., SEM stub no. 531.
*Eatonina (Coriandria) rubicunda* sp. nov. **e.** shell — 1.28 mm x 0.91 mm, **f.** radula — x2200. Elliston, S.A. SEM stub no. 424.
*Eatonina (Coriandria) fulgida* (Alder). **g.** shell — 1.04 mm x 0.72 mm, **h & i.** opercula — both x140. Falmouth, England, SEM stub no. 173. **j.** radula — x2200. Torquay, England, SEM stub no. 423.
*Eatonina (Coriandria) cossurae* (Calcara). **k.** shell — 1.13 mm x 0.70 mm, **l.** operculum — x120, **m.** radula (central — x2800. **n.** radula — x1600. Palermo, Sicily, Italy, SEM stub nos 141 (shell), 144 (operculum & radula).

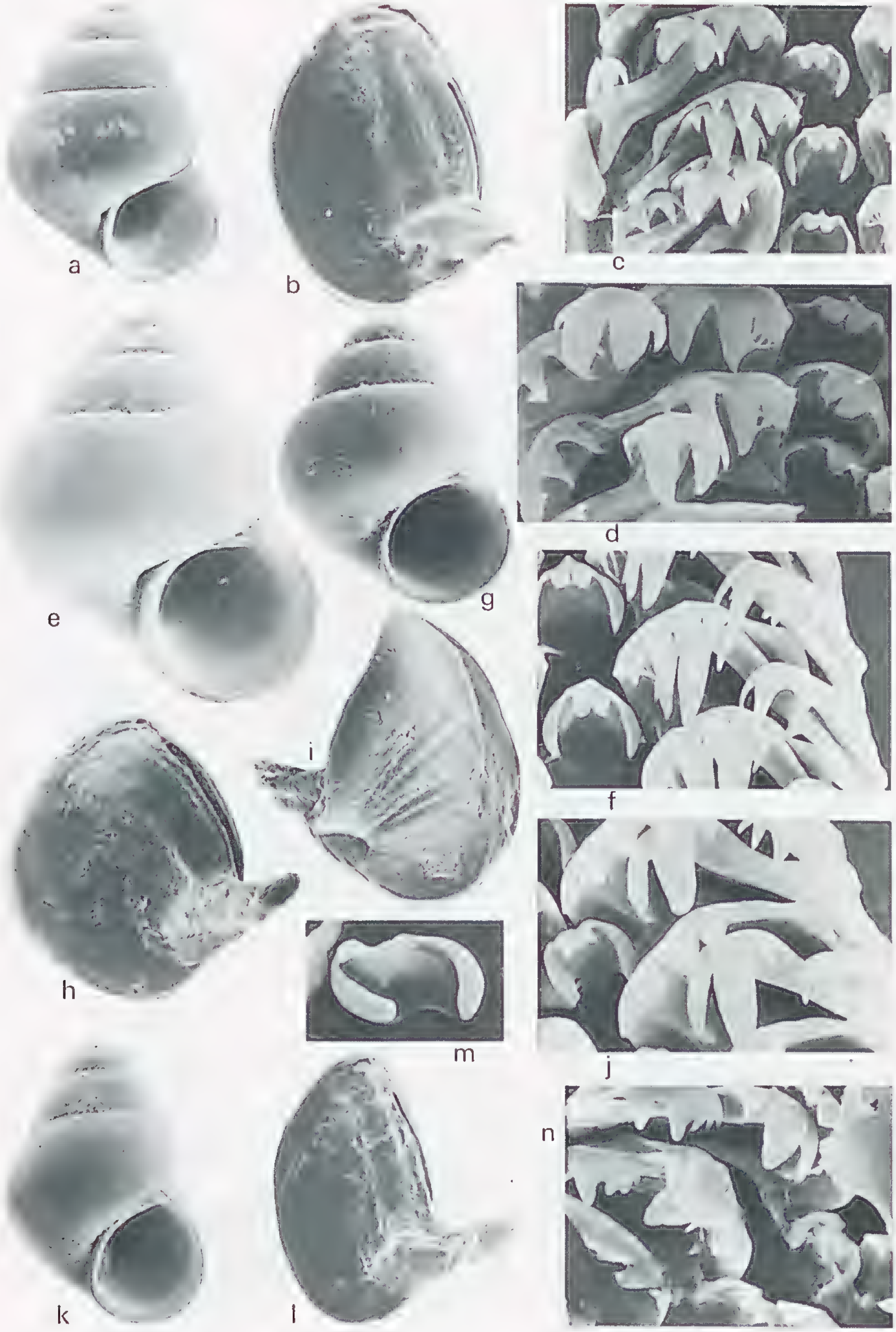
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Fig. 12

*Eatoniopsis (Rufodardanula) castanea* (Laseron). **a.** shell — 1.18 mm x 0.77 mm, **d.** radula — x4000, **e.** radula — x2000. Fairlight, Sydney, N.S.W. SEM stub no. 137. **b.** operculum — x60. Long Reef, Sydney, N.S.W., SEM stub no. 28. **c.** operculum — x140. Nambucca Heads, N.S.W., SEM stub no. 134. *Eatoniopsis (Rufodardanula) porcellana* sp. nov. **f.** shell — 0.92 mm x 0.60 mm, **g.** operculum — x180, **h.** radula — x2400. One Tree Is., Qld, SEM stub nos 263 (operculum & radula), 463 (shell). *Eatoniopsis (Rufodardanula)* cf. *porcellana* sp.nov. **i.** operculum — x270. Heron Is., Qld, SEM stud no. 478. *Eatoniopsis (Rufodardanula) spadix* Ponder. **j.** shell — 0.92 mm x 0.60 mm, **k.** operculum — x140, **l.** radula — x2600. Goat Island Beach, Leigh, New Zealand, SEM stub no. 466.

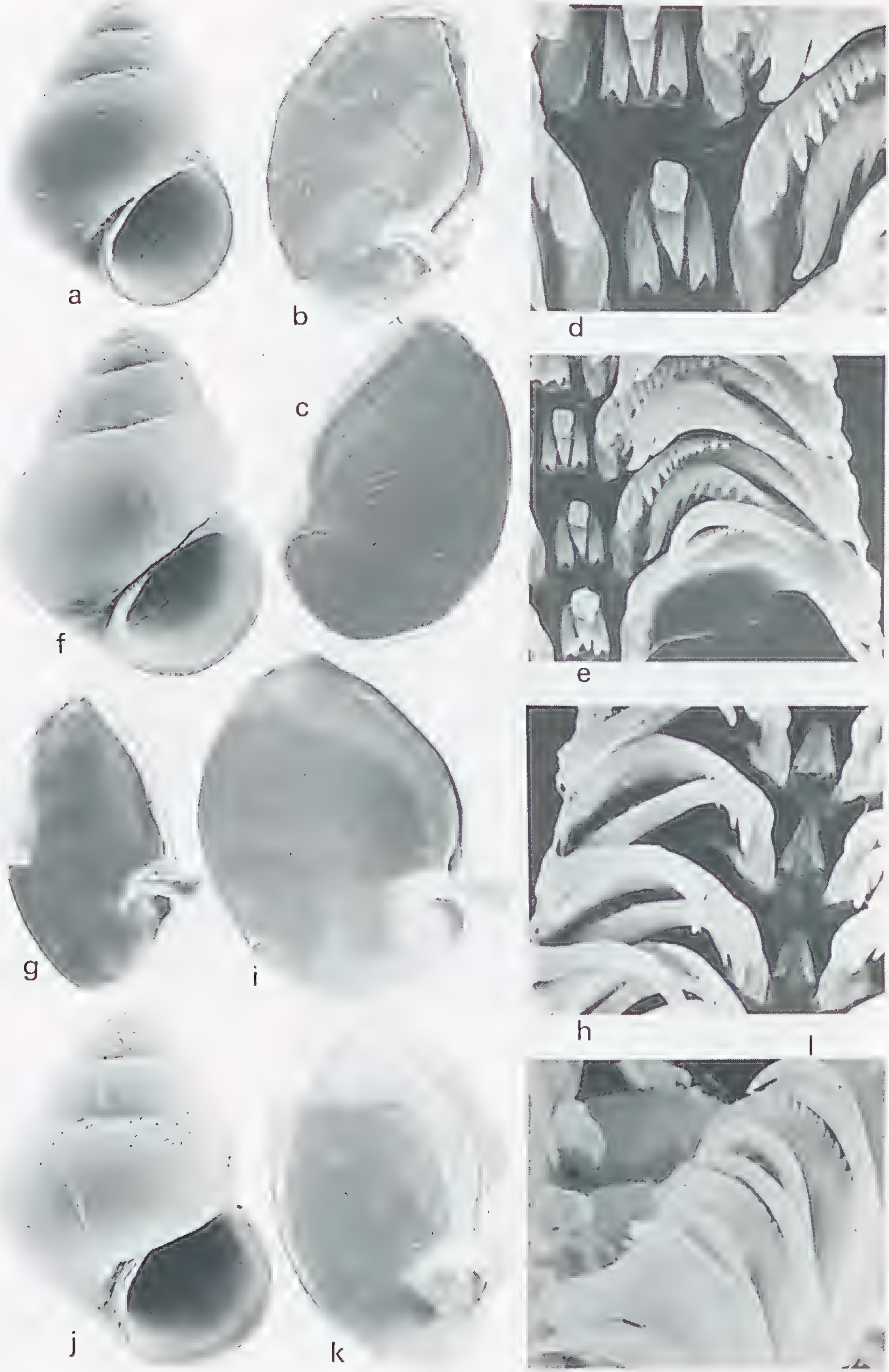
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Fig. 13

*Eatoniopsis (Boogina) voorwindei* sp. nov. **a.** shell — 1.42 mm x 1.00 mm, **b.** operculum — x110, **c.** radula (central) — x4300, **d.** radula — x1900, **e.** radula — x2100. Green Cape, N.S.W., SEM stub no. 432.
*Eatoniopsis (Eatoniopsis)* cf. *edwardiensis* (Watson). **f.** shell — 1.70 mm x 1.35 mm. Pointe Geologie Arch., Terre Adélie, Antarctic, SEM stub no. 500. **g.** operculum — x90, **h.** radula (central) — x2800, **i.** radula — x1700. Robertsons Bay, Duke of York Is., Antarctic, SEM stub no. 431.
*Eatoniopsis (Eatoniopsis) paludinoides* (Smith). **j.** shell — 1.90 mm x 1.35 mm, **k & l.** opercula — both x70, **m.** radula (central) — x2700, **n.** radula — x560. Robertsons Bay, Duke of York Is., Antarctic, SEM stub nos 429 & 430 (n).

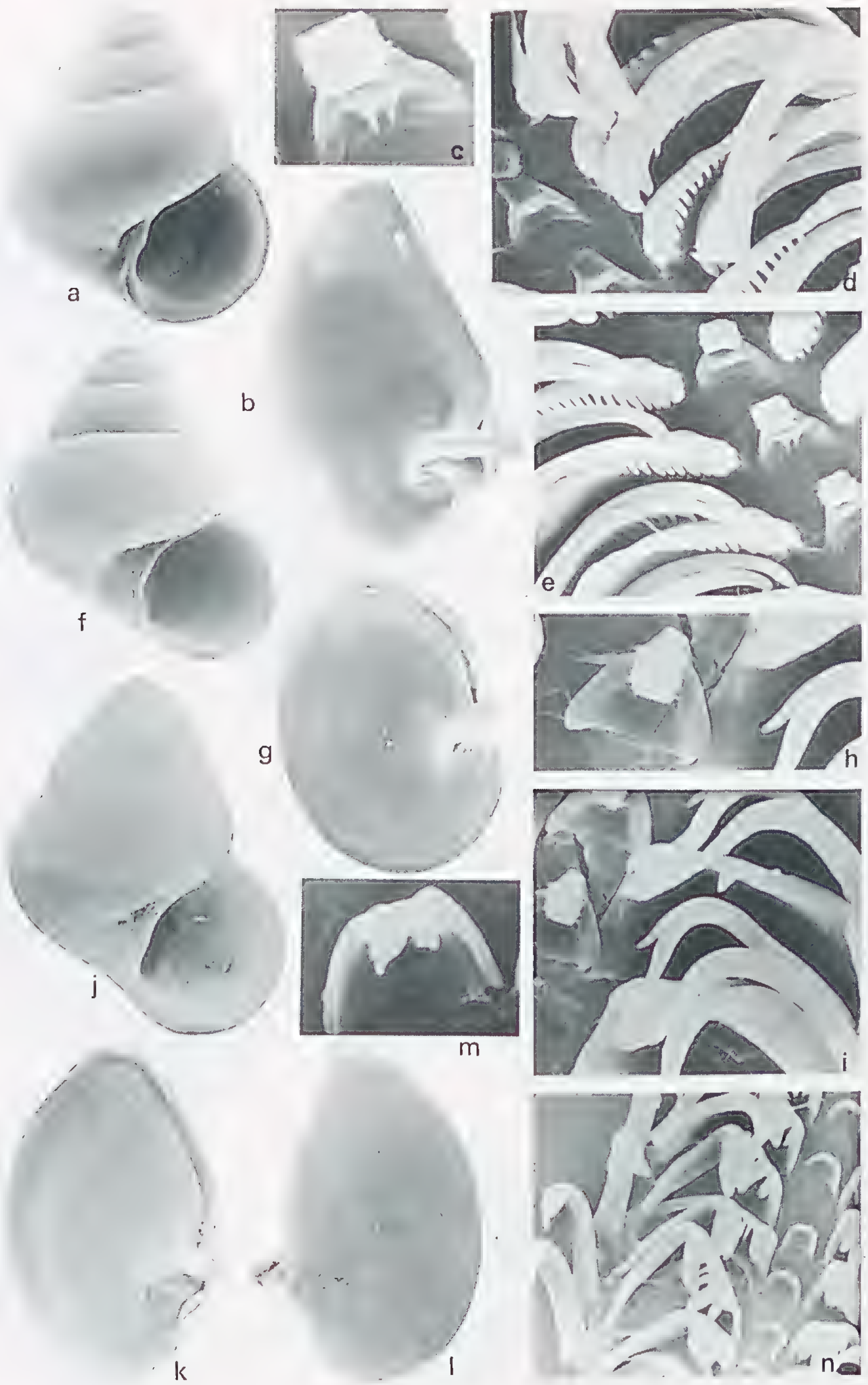
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Fig. 14

*Eatonina (Mistostigma) albida* (Carpenter). **a.** shell — 1.12 mm x 0.84 mm. N. of Ensenada, Baja California, Mexico, SEM stub no. 141. **b.** operculum — x100, c. radula — x960. Todos Santos Is., Baja California, Mexico, SEM stub no. 185.

*Eatonina (Eatonina) atomaria* (Powell). **d.** shell — 1.00 mm x 0.76 mm, **e.** operculum — x140, **f.** radula (central) — x3600. **g.** radula — x1300. High Is., Taruikura Bay, Whangerei Head, New Zealand, SEM stub no. 435.

*Eatonina (Mistostigma) atacamae* Marincovich **h.** radula — x770, **i.** radula (central tooth) — x1400. Iquique, Chile, SEM stub no. 434.

*Eatonina (Eatonina) pusilla* Thiele. **j.** shell — 1.32 mm x 0.96 mm, **k & l.** opercula — both x110, **m.** radula — x960. Millers Pt., South Africa, SEM stub no. 530.

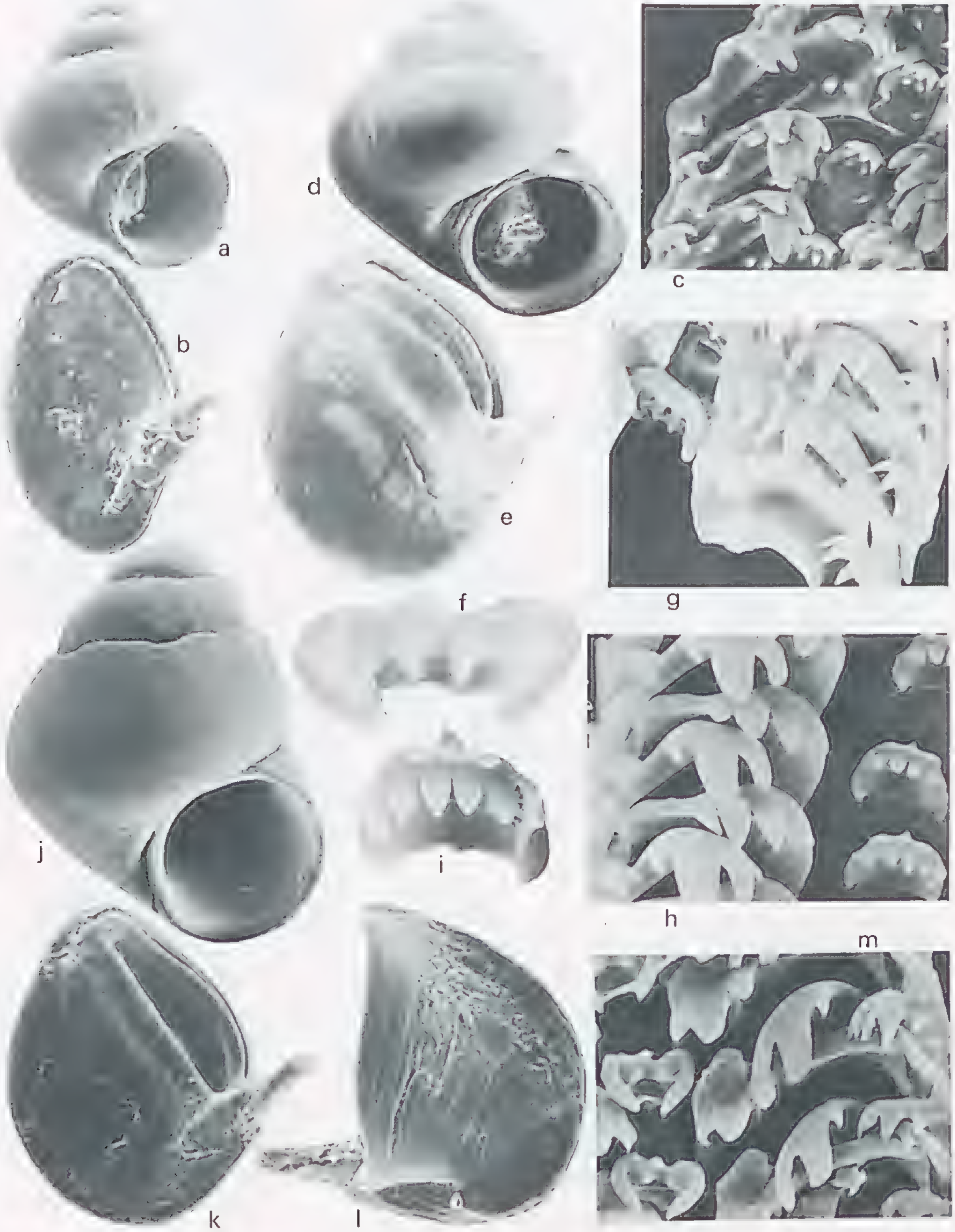
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Fig. 15

*Eatoniopsis (Pilitonia) translucida* sp. nov. **a.** shell — 0.48 mm x 0.62 mm, **b.** operculum — x190. Tanna Is., New Hebrides, SEM stub No. 139.

*Eatoniopsis (Pilitonia) westralis* sp. nov. **c.** shell — 0.80 mm x 0.80 mm, **d.** operculum — x130, **e.** radula — x2200. Mississippi Bay, S.W.A., SEM stub no. 149. **f.** operculum — x130, **g.** radula — x1800. Rottnest Is., W.A., SEM stub no. 275.

*Tubbreva insignificans* sp. nov. **h.** operculum — x190. Carnac Is., off Fremantle, W.A., SEM stub no. 491.

*Tubbreva parva* sp. nov. **i.** operculum — x190. Caloundra Head, Qld, SEM stub no. 458.

*Tubbreva exigua* (Ponder). **j.** shell — 1.00 mm x 0.58 mm, **k.** operculum — x130. Island Bay, Wellington, New Zealand, SEM stub no. 170.

*Eatonina (Captitonia) lirata* sp. nov. **l.** operculum — x220, **m.** radula — x2200. Garden Is., off Fremantle, W.A., SEM stub no. 337.

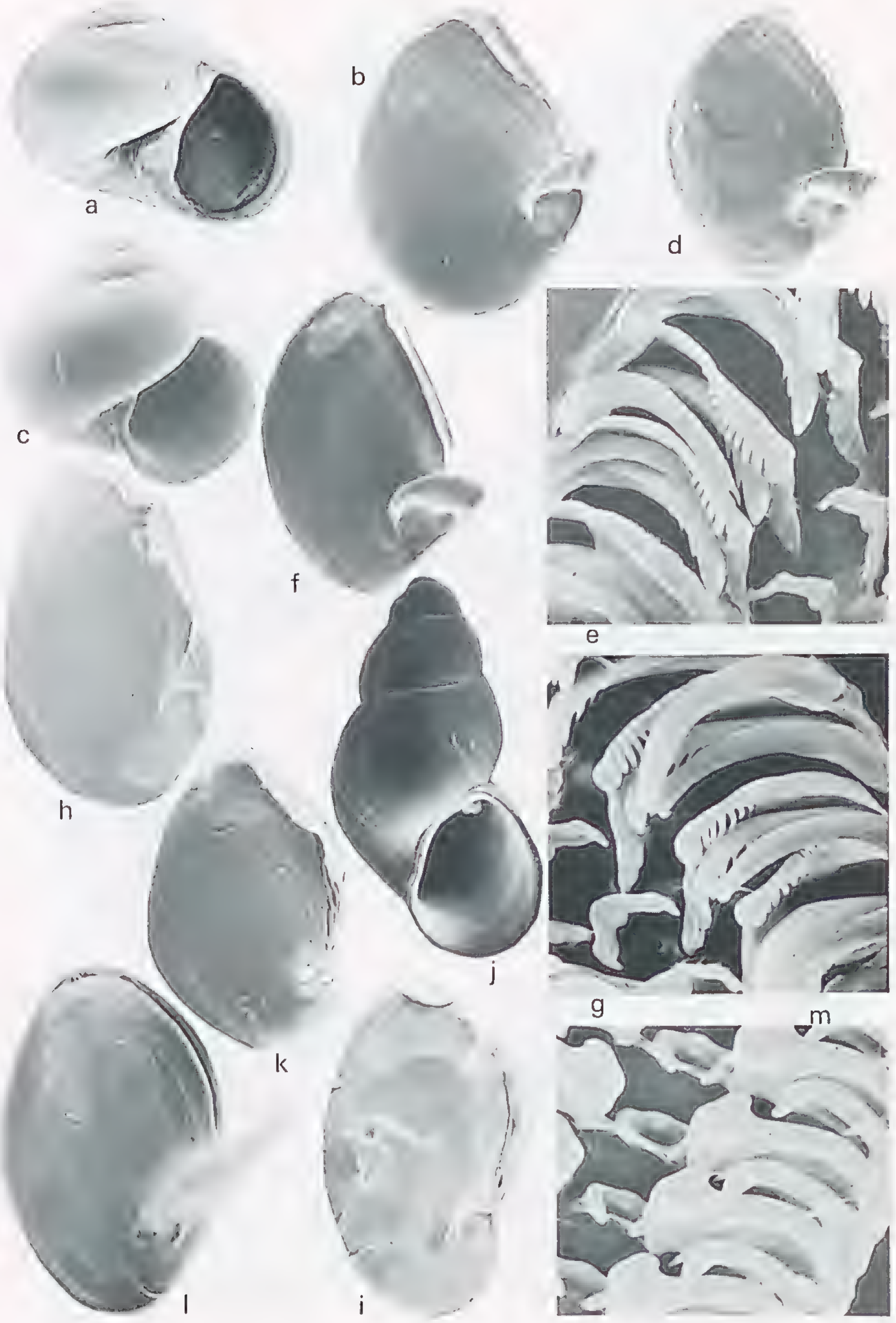
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Fig. 16

*Pseudopisinna balteata* sp. nov. **a.** shell — 0.86 mm x 0.53 mm, **e.** operculum — x240. Basilisk Passage, Port Moresby, Papua New Guinea, SEM stub no. 133. **b.** shell — 0.84 mm x 0.51 mm, **f.** operculum — x270. Yam Is., Torres Strait, Qld, SEM stub no. 427. **c.** shell — 0.92 mm x 0.58 mm, **d.** operculum — x270, **g.** radula — x2000. Croissant Reef, off Nouméa, New Caledonia, SEM stub no. 261.

*Pseudopisinna costata* sp. nov. **h.** shell — paratype, **i.** operculum — x270, **j.** radula — x1700. Houtman Abrolhos, W.A., SEM stub no. 174.

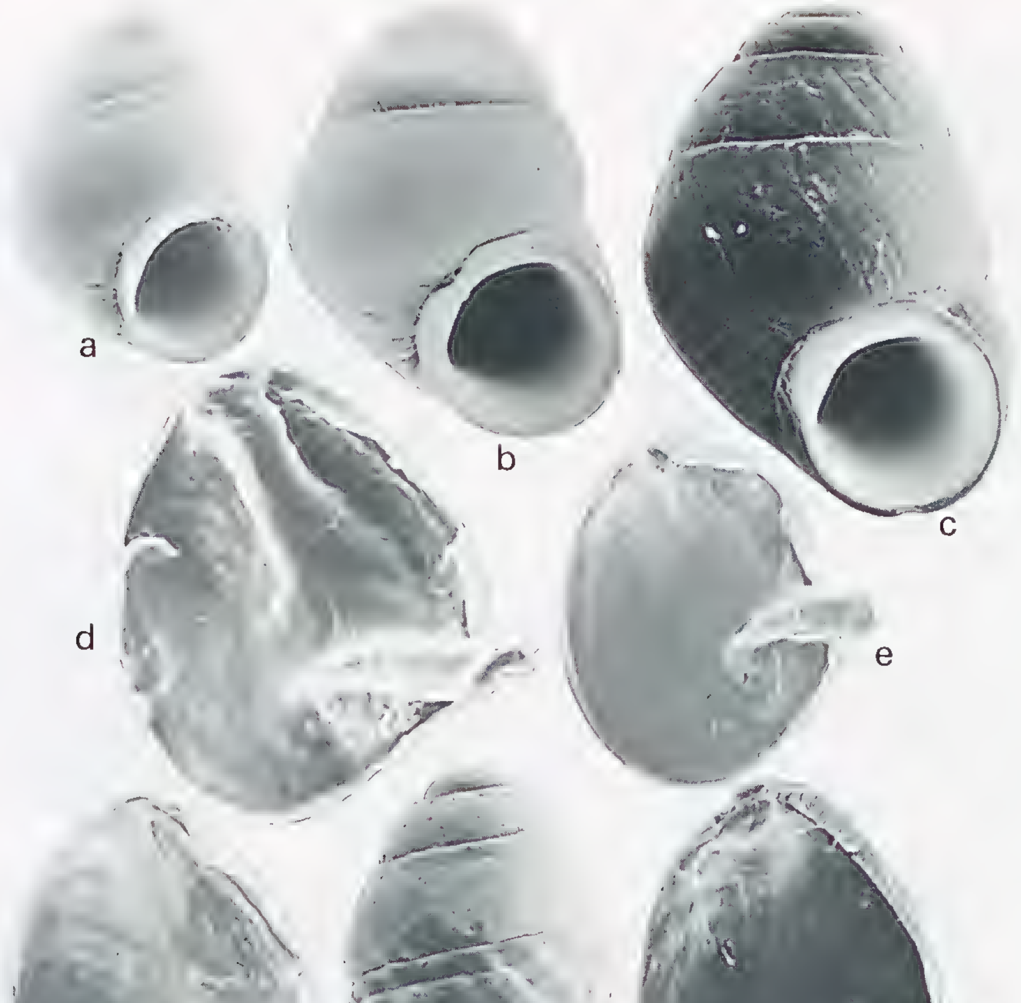
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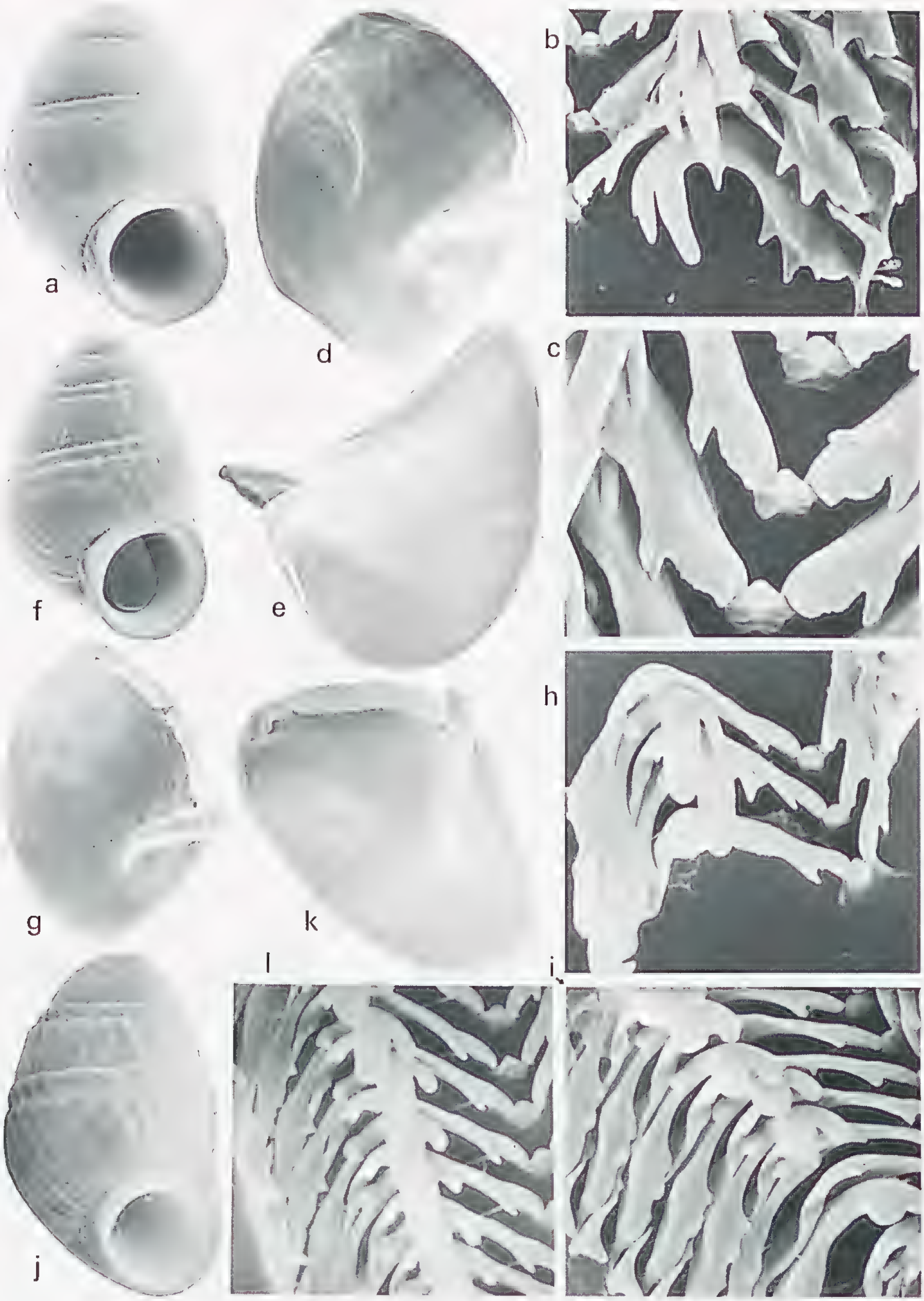
Fig. 17

*Pseudopisinna gregaria gregaria* (Laseron) **a.** shell — 1.02 mm x 0.60 mm, **b.** radula — x2300, **c.** radula — x4600. Forster, N.S.W., SEM stub no. 172. **d & e.** opercula — both x230. Honeymoon Beach, Jervis Bay, N.S.W., SEM stub no. 333. **f.** shell — 1.13 mm x 0.64 mm, **g.** operculum — x170, **h & i.** radulae — both x1400. Yallingup, S.W.A., SEM stub no. 131.
*Pseudopisinna gregaria rugifera* subsp. nov. **j.** shell — 0.94 mm x 0.52 mm, **k.** operculum — x250, **l.** radula — x2300. Heron Is., Qld, SEM stub no. 208.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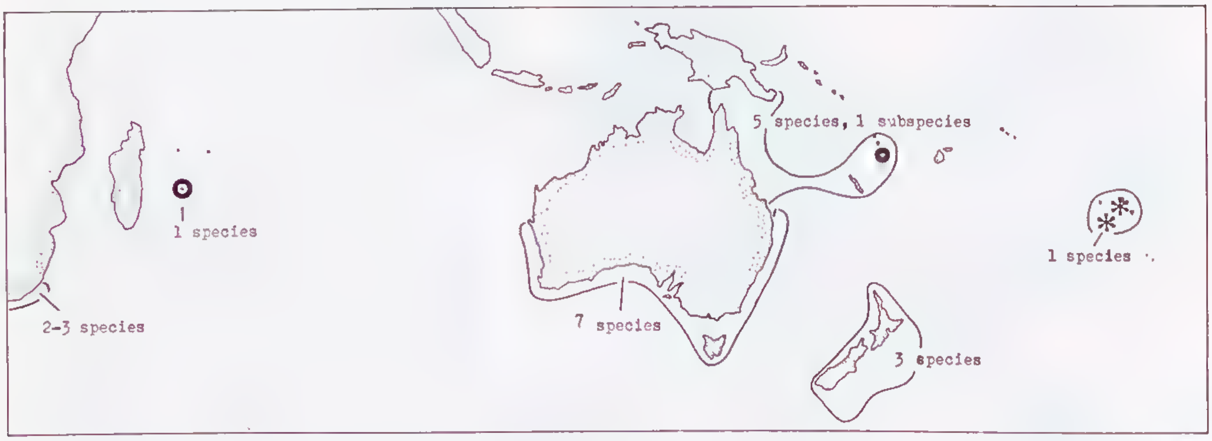

Fig. 18. Distribution of species of *Eatonina (Eatonina).* ○ *Eatonina (E.) pulicaria pulicaria* (Fischer), ● *E. (E.) pulicaria pacifica* subsp. nov., * *E. (E.) lactea* sp. nov.

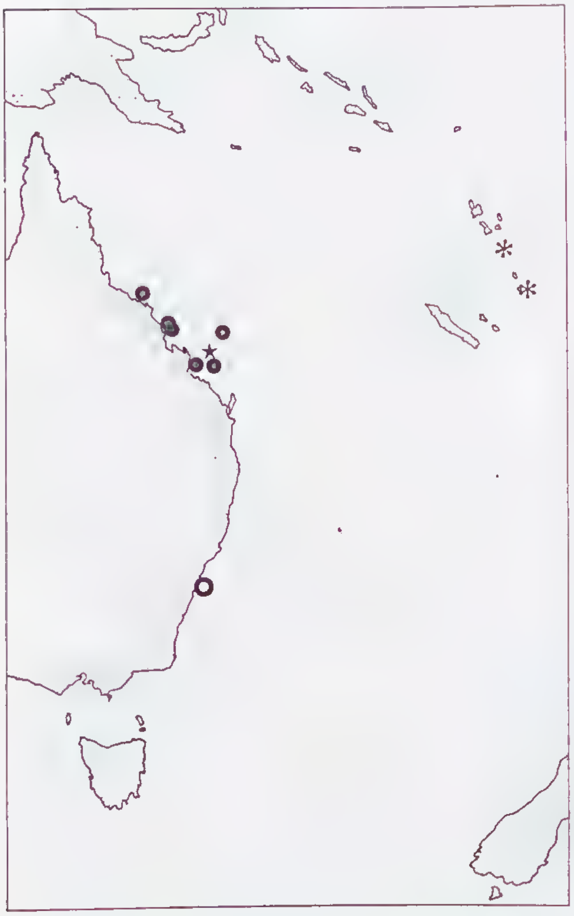

Fig. 19 Distribution of *Eatonina (Eatonina)* species. ★ *E. (E.) ardeae.* sp. nov., ● *E. (E.) capricornea* (Hedley), * *E. (E.) colorata* sp. nov., ○ *E. (E.) hedleyi* sp. nov.

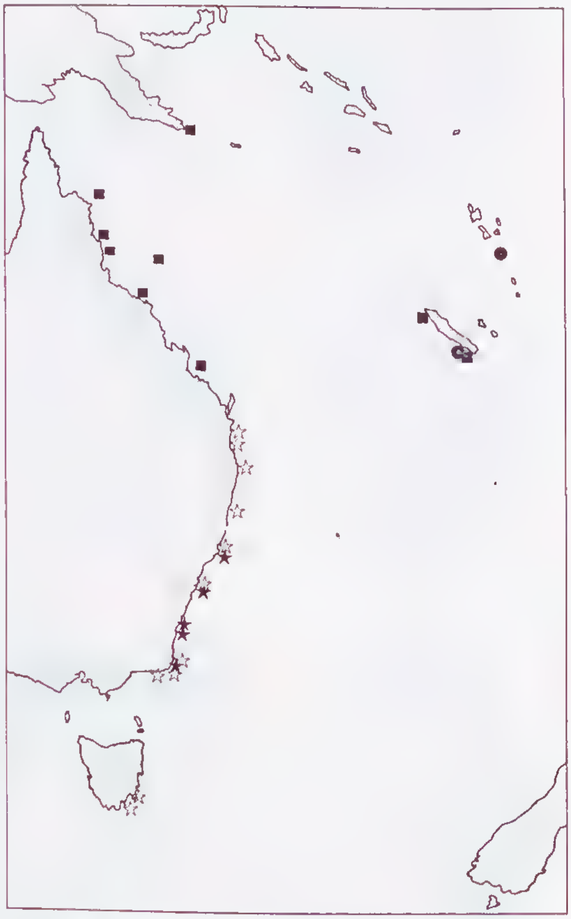

Fig. 20. Distribution of *Eatonina (Eatonina)* species. ● *E. (E.) heliciformis* sp. nov., ☆ *E. (E.) hutchingsae* sp. nov., ■ *E. (E.) lunata* (Laseron), ★ *E. (E.) rubrilabiata* sp. nov.

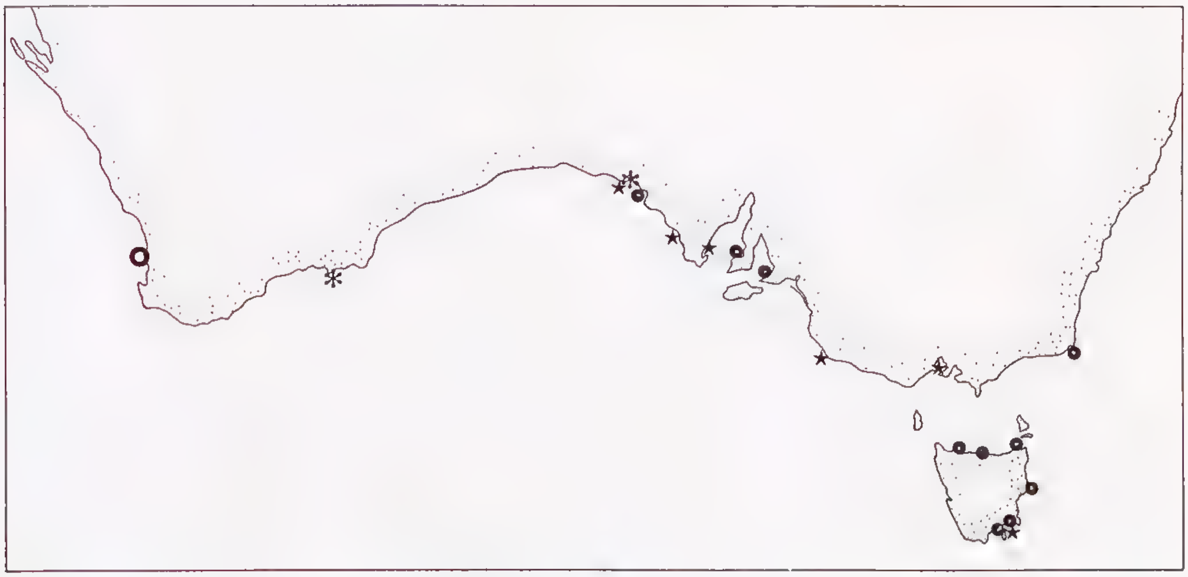

Fig. 21 Distribution of *Eatonina (Eatonina)* species. ● *E. (E.) condita* sp. nov., ★ *E. (E.) sanguinolenta* sp. nov., * *E. (E.) shirleyae* sp. nov., ○ *E. (E.) striata* sp. nov.

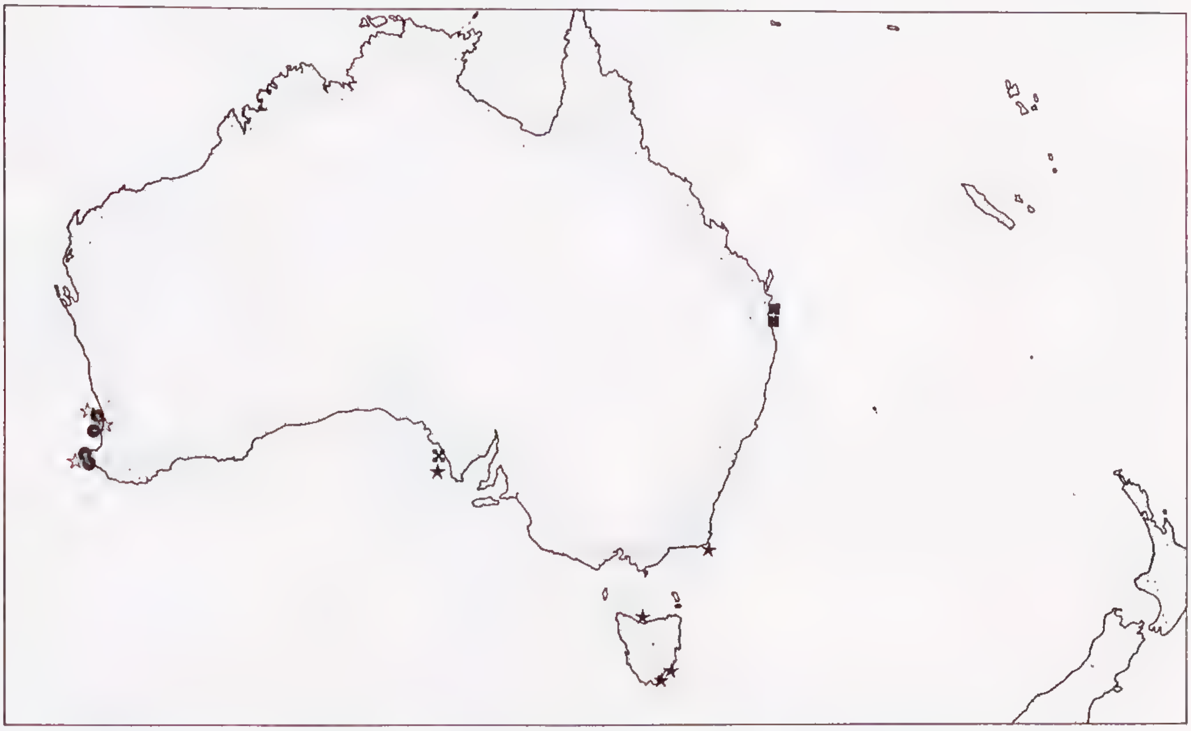

Fig. 22. Distribution of *Eatonina (Coriandria), Eatonina (Captitonia)* and *Tubbreva* species. ★ *E. (Coriandria) fulvicolumella* sp. nov. * *E. (C.) rubicunda* sp. nov., ● *E. (Captitonia) lirata* sp. nov., ☆ *Tubbreva insignificans* sp. nov., ■ *Tubbreva parva* sp. nov.

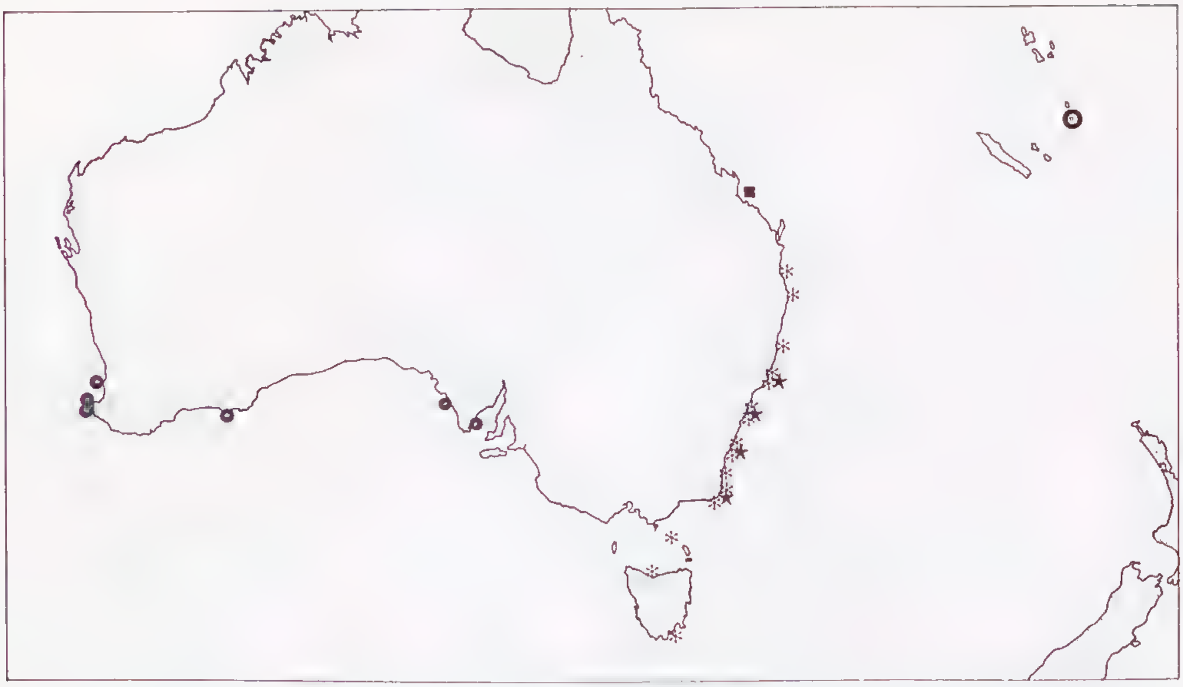

Fig. 23. Distribution of *Eatoniopsis (Boogina)*, *(Rufodardanula)* and *(Pilitonia)* species. ★ *E. (B.) voorwindei* sp. nov., **E. (R.) castanea* (Laseron), ■ *E. (R.) porcellana* sp. nov., ○*E. (P.) translucida* sp. nov., ● *E. (P.) westralis* sp. nov.

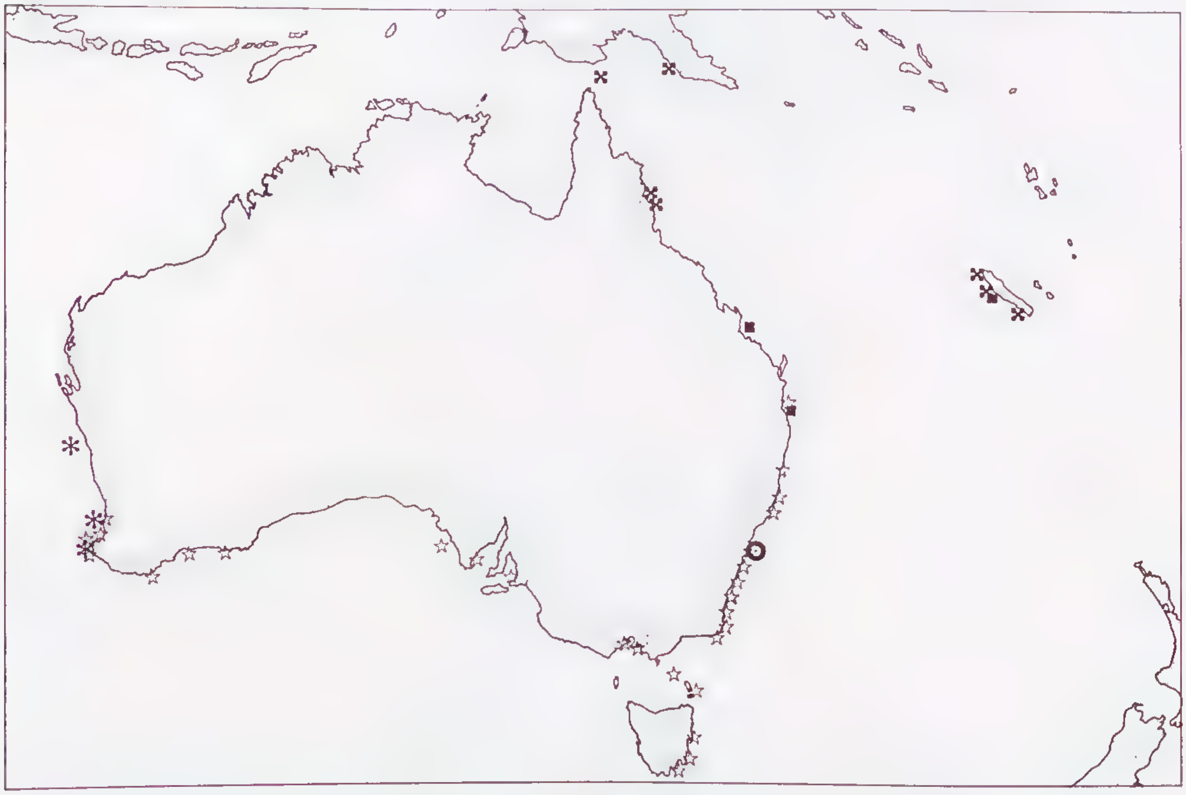

Fig. 24. Distribution of *Pseudopisinna* species. ○*P. (?) alvea* (Laseron), ★*P. balteata* sp. nov., **P. costata* sp. nov., ☆ *P. gregaria gregaria* (Laseron), ■ *P. gregaria rugifera* subsp. nov.

# A NEW SPECIES OF *MORETHIA* (LACERTILIA: SCINCIDAE) FROM NORTHERN AUSTRALIA, WITH COMMENTS ON THE BIOLOGY AND RELATIONSHIPS OF THE GENUS

ALLEN E. GREER

The Australian Museum, Sydney

## ABSTRACT

*Morethia* is a genus of lygosomine skinks endemic to Australia. This paper provides a description of a new species of *Morethia* from northern Australia, a diagonsis of the genus, and a discussion of its intra and intergeneric relationships. It also includes a key to the eight currently recognized species of *Morethia* and notes on their colour pattern, reproduction, behaviour, habitat and distribution.

## A NEW SPECIES OF MORETHIA

In his revision of the Western Australian species of the endemic Australian genus *Morethia,* Storr (1972) noted that the form *ruficauda* was "replaced by an undescribed race" in the far north of the Northern Territory. A few years later while reviewing the genus, I "rediscovered" this undescribed form and interpreted it as a distinct species. Dr Storr has graciously allowed me to describe this species, and in appreciation of his original contribution to the taxonomy of the genus (Storr 1972), I take pleasure in naming it

### *Morethia storri* New Species

Figs 1, 2 (top), and 9

HOLOTYPE: Northern Territory Museum R 1815 — 4.5 km. S. of Noonamah, Northern Territory (12°40′ S., 131°04′ E.). Collected by Messrs G. F. Gow and R. W. Wells on 10 November 1975.

PARATYPES: Unless specifically mentioned otherwise, all localities are in the extreme northern part of the Northern Territory.

Australian Museum: R 12384 — Yirrkala; R 17411 — Port Keats Mission; R 37225 — Koongarra, Mt. Brockman Range; R 41960 — Maningrida Settlement; R 71991 — Yirrkala; R 72862 — appox. 16 km. S.E. of Daly River Police Station (by road); R 88631, 88791, 88850 and 88988 — Jabiluka Project Area (12°33′ — 12°35′S., 132°55′ — 132°57′E.).

Australian National Wildlife Collection: R 695 — Leanyer Swamp, RAAF Bombing Range, Darwin; R 1826 — Berrimah, Darwin.

South Australian Museum: R 1117 — Groote Eylandt; R 1130 A-B — Roper River (it is uncertain whether the township or the river is meant, *fide* Dr T. Houston in letter of 29 March 1977); R 13535 — Bing Bong Station near Boorroloola.

Northern Territory Museum: R 2715 — Berry Springs Reserve; R 2731-2732 — 32.5 km. S.E. of Noonamah; R 2864 — Millner, Darwin.

United States National Museum: 128635 — Yirrkala.

Western Australian Museum: R 23481 — Nightcliff, Darwin; R 23517 — Rapid Creek, Darwin; R 58498 — Lombadina Creek, Western Australia (16°34′S., 122°48′E.).

DIAGNOSIS: *Morethia storri* differs from all other *Morethia* in the following combination of characters: supranasal scale fused to nasal without trace of suture; lower

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eyelid completely fused to underside of supraocular shelf (i.e., no palpebral slit); supraciliaries five (first four large and last small) and projecting behind first, second, and third supraoculars, and colour pattern consisting of a more or less uniform plain or faintly longitudinally striped dorsum and a distinct dark lateral stripe bordered above by a thin light dorsolateral stripe.

DESCRIPTION: In general aspect *storri* is a small (maximum snout-vent length = 38 mm), pentadactyl, spectacle-eyed skink with either a uniformly brown or faintly longitudinally striped dorsum and a distinct dark lateral stripe bordered above and below by more or less distinct, narrow white stripes.

Rostral prominent in dorsal view, its posterior edge slightly convex; frontonasal slightly wider than long, usually forming a narrow suture with the rostral (frequency = .94) and a narrow suture with the frontal (.85); prefrontals large and either narrowly separated (.85) or in contact (.15); frontal longer than wide; frontoparietals and interparietal fused into a single scale which bears a parietal eye spot in its posterior lobe; parietals narrow, in medial contact behind the fused frontoparietal — interparietal; parietals bordered posterolaterally by the single upper secondary temporal and the enlarged anterior nuchal.

Supranasal fused anteriorly to nasal without trace of a suture or groove and fused posteriorly to postnasal with a horizontal groove which may indicate the position of the former suture; loreals two; anterior loreal much deeper than long, posterior loreal much lower than anterior loreal and slightly longer than deep; preoculars two, suboculars none and postoculars three; supraciliaries five, first four large, fifth very small; second supraciliary projects medially to partially separate first and second supraoculars, third supraciliary projects to partially separate second and third supraoculars and fourth supraciliary separates third and fourth supraoculars; lower eyelid with a large clear spectacle surrounded by small periocular scales; no palpebral slit; primary temporals two, subequal; secondary temporals two, upper much larger than lower; supralabials seven or, rarely, eight with fifth or, rarely, sixth below centre of eye; mental followed by postmental and two chin scales in medial contact; postmental in contact with first two infralabials on each side; external ear opening vertically suboval, approximately one-quarter to one-third size of spectacle, without projections.

A single pair of transversely enlarged nuchal scales; body scales smooth, subequal in size dorsally and in 24-28 ($\bar{X}$ = 26.2, mode =26) longitudinal rows at midbody; scales in paravertebral row 54-58 ($\bar{X}$ =56.1) counted from level of posterior edge of thigh forward to parietals; medial pair of preanals only slightly larger than most immediately adjacent preanals; limbs pentadactyl; fourth toe covered by a single row of scales above and by 17-21 ($\bar{X}$ =19.4) obtusely keeled lamellae below.

Snout-vent length =17-38 mm; foreleg .25-.35 times and rear leg .36-.47 times SVL (N = 14), respectively; complete tail 1.32-1.76 times SVL (N = 3).

COLOUR IN PRESERVATIVE: Dorsum of head and body usually more or less uniform medium brown but occasionally, dorsum of body faintly light and dark striped; sides of head and body with a distinct narrow light dorsolateral stripe extending from above eye onto base of tail, a distinct dark brown lateral stripe from loreals to base of tail, and a distinct narrow light lower lateral stripe from labials to rear leg; venter immaculate; lower labials with a few scattered brown spots; a small white post-femoral spot at junction of rear leg and base of tail.

COLOUR IN LIFE: Details on the colour of *storri* in life come from three sources: a transparency taken by Dr H. G. Cogger of a female from Koongarra (A.M. R 37225); the

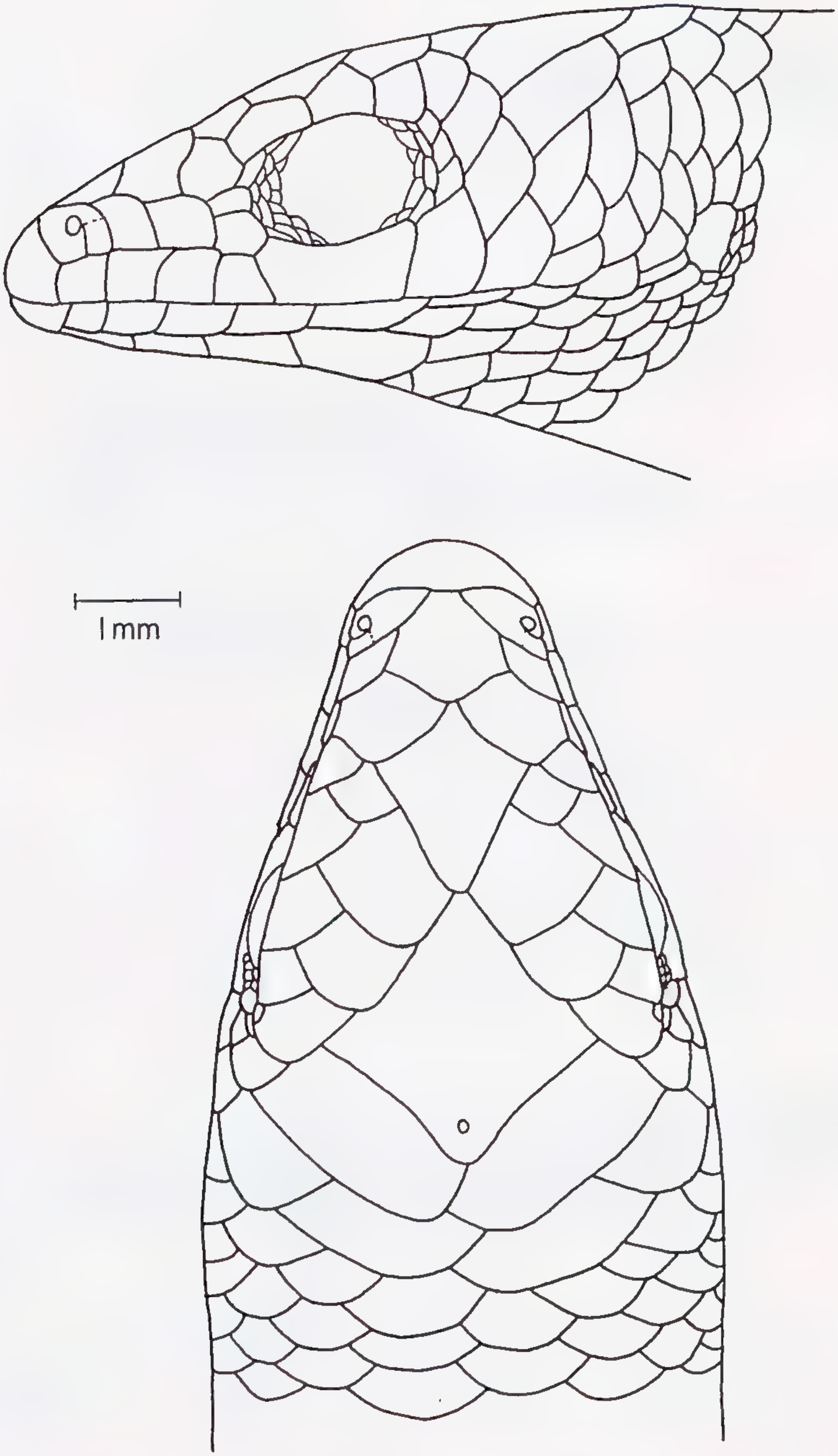

Fig. 1. Dorsal and lateral views of the head of *Morethia storri* (S.A.M. R 13535) from Bing Bong Station, near Borroloola, N.T.

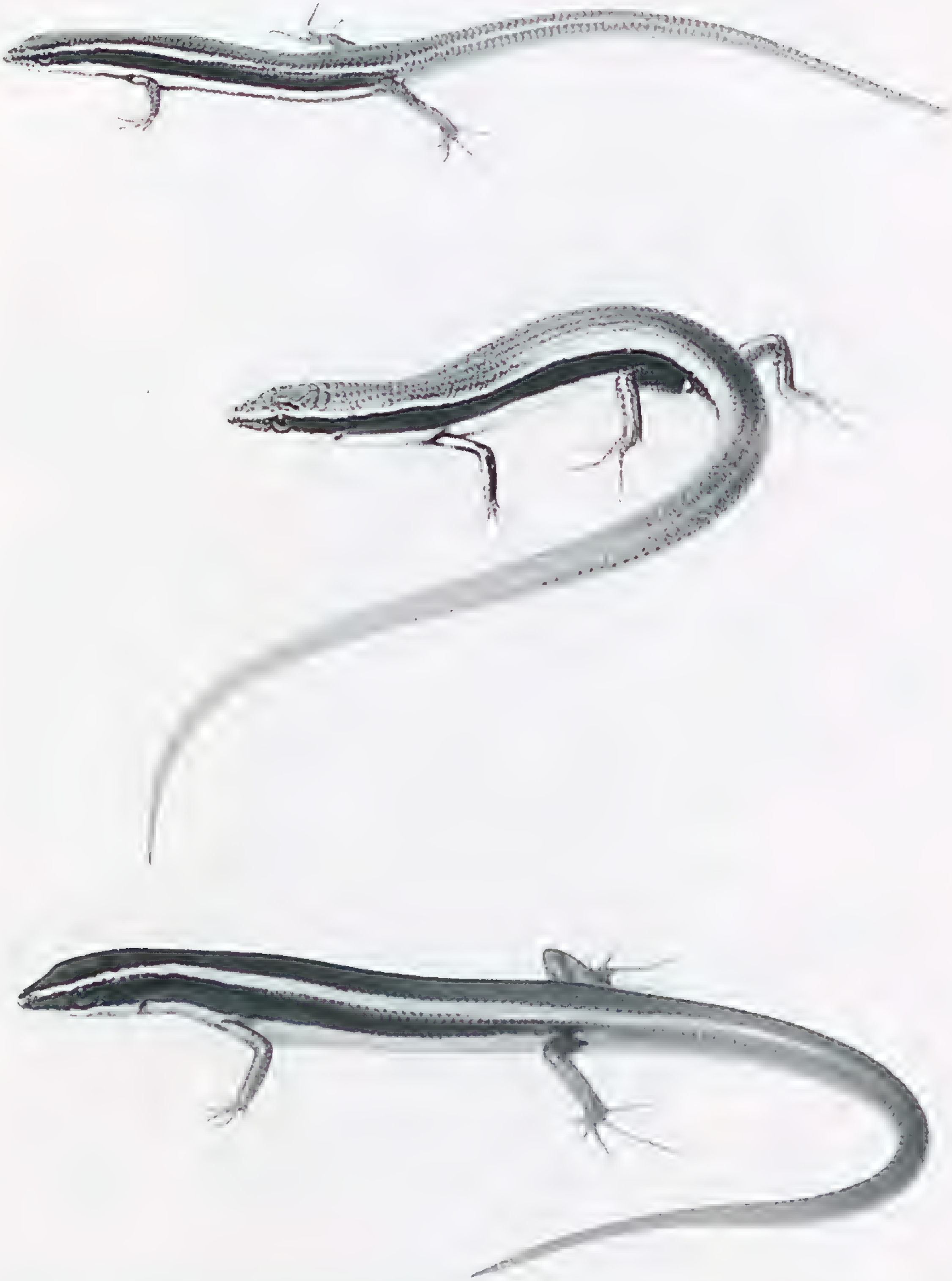

Fig. 2. Photographs of *Morethia storri* and its two most similar relatives. Top: *M. storri* (A.M. R 37225) from Koongarra, Mt. Brockman Range, N.T.; middle: *M. taeniopleura* from Townsville, Qld., and bottom: *M. ruficauda* from 16 km. S.E. Daly River Police Station, N.T.

fading colour in an unsexed specimen from Berrimah (A.N.W.C. R 1826) preserved five weeks prior to observation, and notes made by Mr Ross Sadlier on a male from the Jabiluka Project Area (A.M. R 88631). The specimen in the transparency shows russet to dull brick red colour on the dorsal surfaces of the tail and hind legs; the tail colour is most intense distally and diminishes rapidly over the base. The preserved specimen shows raspberry pink colour over all but the very basal part of the tail. This colour is also evident, albeit more diffusely, over the rear legs and distal half of the foreleg. No other colour is evident in either specimen. The specimen noted in life had pinkish orange colour on the tail (less intense anteriorly), throat and tip of snout.

DETAILS OF THE HOLOTYPE: The holotype shows the following characters: prefrontals just meet at their medial corners; midbody scale rows, 26; paravertebral scales, 58; subdigital lamellae on fourth toe, 18-19; SVL, 37 mm; unregenerated portion of tail, 32 mm; regenerated portion of tail, 8 mm; length of foreleg, 9.5 mm; length of rear leg, 14 mm.

DISTRIBUTION: The new species is known to date from northern Dampier Land in Western Australia and the broad coastal plain and certain offshore islands in the far northern part of the Northern Territory (Fig. 9). All the known localities are below 150 metres (approx. 500 feet) elevation.

FIELD NOTES: There is relatively little information on the habitat associations of *storri*. According to Mr R. W. Wells (pers. comm.), the holotype (N.T.M. R 1815) was in the roadside verge of a grassy open woodland with scattered cycads. At the time of collection at the end of the dry season, the scattered low clumps of "dormant" Spear Grass (*Sorghum* sp.) were separated by broad intervals of very dry, firm lateritic soil consisting of small ironstone pebbles. A later visit to this site during the wet season of 1977, however, showed that grass cover may reach a height of 2-3 metres and become extremely dense. Mr Wells also notes that the Berry Springs specimen (N.T.M. R 2715) was in a similar habitat but the soil was locally sandy. According to Dr H. G. Cogger the Koongarra specimen (A.M. R 37225) was found in an *Eucalyptus* woodland on the slightly rolling upper reaches of Deaf Adder Creek. The field notes associated with various specimens also give some indication of the habitats occupied: the Western Australian specimen (W.A.M. R 58498) was found in *Acacia* leaf litter at the edge of vine scrub; the Leanyer Swamp specimen (A.N.W.C. R 695) was found in open grassland on sandy soil while the Berrimah specimen (A.N.W.C. R 1826) was found "under a log in wet grass."

Mr R. Sadlier (pers. comm.) found both *storri* (A.M. R 88631, 88791, 88850 and 88988) and *ruficauda* (R88523, 88663, 88665, 88674-88675, 88836, 88846, 88848, 88949, 88954-88955) in broad sympatry in the Jabiluka Project Area of the Northern Territory but in different habitats: *storri* in open woodland on the sandy and lateritic/sandy soils of the alluvial flats of the Magela drainage and *ruficauda* in woodland on the stony soils of an outlier of the Arnhemland sandstone plateau.

There is one interesting behavioural observation available for *storri*. Mr Wells informs me that the Berry Springs specimen buried itself in loose soil while being pursued. This may be a characteristic evasion response in *Morethia* as I have noted it in *adelaidensis, boulengeri, butleri, lineoocellata, obscura* and *taeniopleura*.

REPRODUCTION: The two females from "Roper River" (S.A.M. R 1130 A-B) are gravid with shelled oviducal eggs which indicate that the species is oviparous, as are all other *Morethia* (see Notes section). One of these females measures 36 mm SVL and contains three eggs, and the other measures 38 mm SVL and contains two eggs. No collection date is available for either specimen.

COMPARISONS WITH OTHER *MORETHIA*: *Morethia storri* shows greatest overall similarity to *taeniopleura* and *ruficauda* but in certain points of squamation it is most similar to *lineoocellata* and *adelaidensis*. Three characters serve to ally *storri* with *taeniopleura* and *ruficauda*. These are (1.) a lower eyelid which is completely fused to the underside of the supraocular shelf instead of only partially fused; (2.) a relatively small body size with a maximum snout-vent length of less than 46 mm instead of 57 mm or more, and (3.) a colour pattern featuring a distinct dark brown lateral stripe bordered above by a distinct light dorsolateral stripe and a relatively uniformly coloured or only faintly longitudinally striped mid-dorsal area[1] instead of a more or less diffuse dark brown lateral stripe or area with no light dorsolateral stripe[2] and usually a mottled, blotched or ocellated mid-dorsal area.

*Storri* is closest to *taeniopleura* in colour pattern in that both species have a thin light dorsolateral stripe separated from its fellow by approximately six scale rows whereas *ruficauda* has a rather wide light dorsolateral stripe separated from its fellow by only three to five scale rows. Furthermore, in both *storri* and *taeniopleura* the dorsolateral light stripes end above the eye whereas in *ruficauda* the stripes run forward to converge on the snout.

*Storri* is more similar to *ruficauda* than *taeniopleura*, however, in the relative size of the supraciliaries; both *storri* and *ruficauda* usually have four very large supraciliaries followed by a very small fifth whereas *taeniopleura* usually has five relatively large supraciliaries (Fig. 3).

*Storri* may be readily distinguished from both *ruficauda* and *taeniopleura* in having the anterior part of the supranasal fused to the nasal instead of completely separate and in having the supraciliaries projecting behind the first, second and third supraoculars instead of just the first and second (Table 1 and Fig. 3).

In showing these last two characters in combination, *storri* is similar to *lineoocellata* of Western Australia, but *storri's* uniform or only faintly striped brown dorsum, distinct light dorsolateral stripe and distinct dark lateral stripe will instantly distinguish it from *lineoocellata* with its olive-grey or olive-brown and often variegated dorsum, usual absence of a light dorsolateral stripe, and only vague dark lateral stripe or area.

*Storri* is also similar to *adelaidensis* in having the supraciliaries projecting behind the first, second, and third supraoculars (Fig. 3), but it differs from this species in having the anterior part of the supranasal fused to the nasal instead of completely separate and a distinct dark lateral stripe bordered above by a distinct light dorsolateral stripe instead of an only ill-defined dark lateral area and no distinct light dorsolateral stripe.

A key to all the currently recognized species and subspecies of *Morethia* comprises a separate later section of this paper.

## DIAGNOSIS OF THE GENUS *MORETHIA*

The genus *Morethia* is a member of the *Eugongylus* subgroup of the *Eugongylus* group of lygosomine skinks (Greer 1979). This subgroup is centred over the Australian Region and comprises the following genera in addition to *Morethia*: *Anotis*, *Cryptoblepharus*, *Emoia*, *Eugongylus*, *Leiolopisma* (including *Pseudemoia*), *Phoboscincus*, *Proablepharus* and *Tachygyia*.

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1. The distinct light mid-dorsal stripe of *ruficauda exquisita* is an exception, but it is in no way similar to the mid-dorsal colour pattern of the other *Morethia*.

2. A few *lineoocellata* have a distinct light dorsolateral stripe.

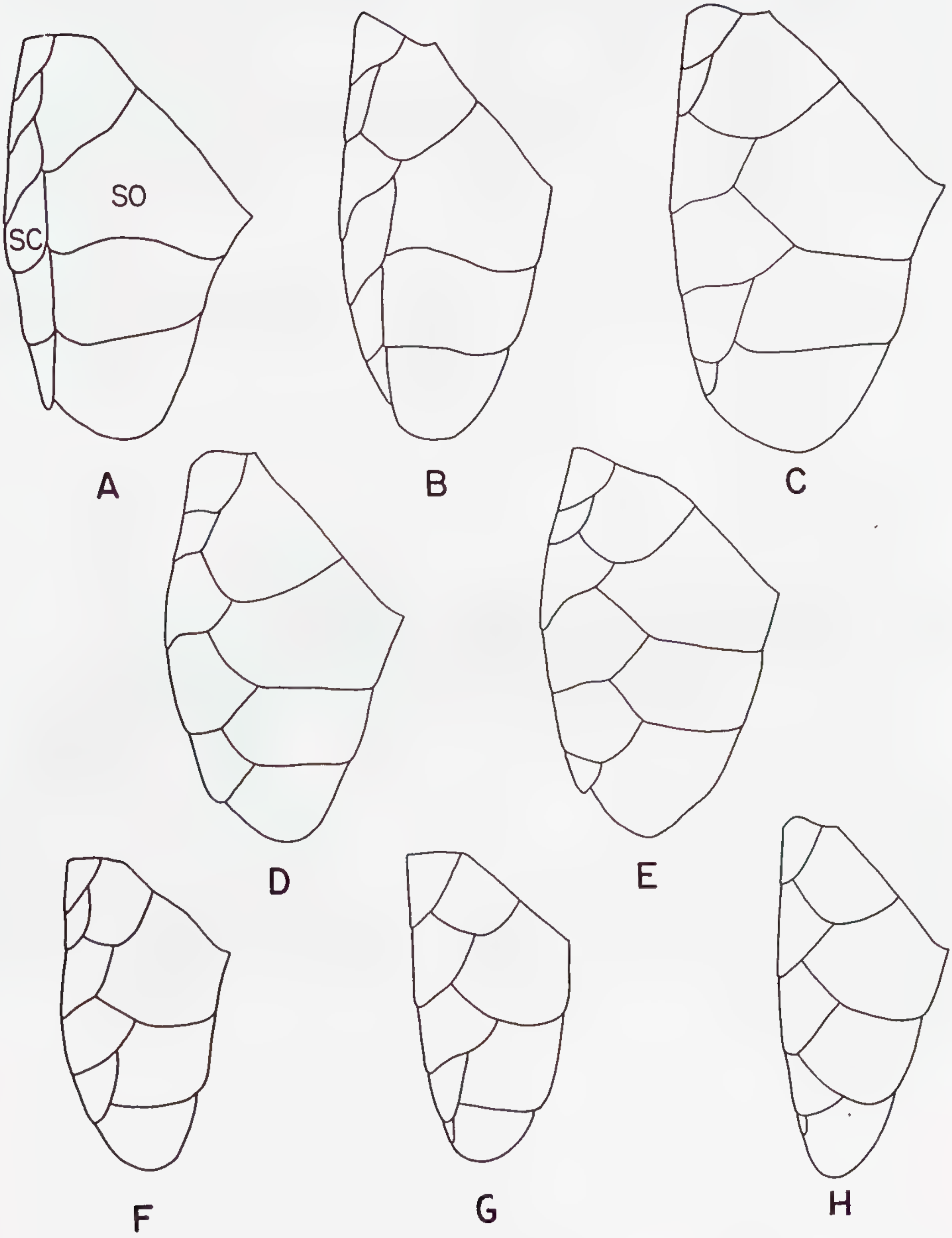

Fig. 3. Line drawings of the supraocular (SO) and supraciliary (SC) scales on the left side of the head in the eight species of *Morethia*. The species are as follows: A — *butleri*, B — *boulengeri*, C — *obscura*, D — *adelaidensis*, E — *lineoocellata*, F — *taeniopleura*, G — *ruficauda*, H — *storri*.

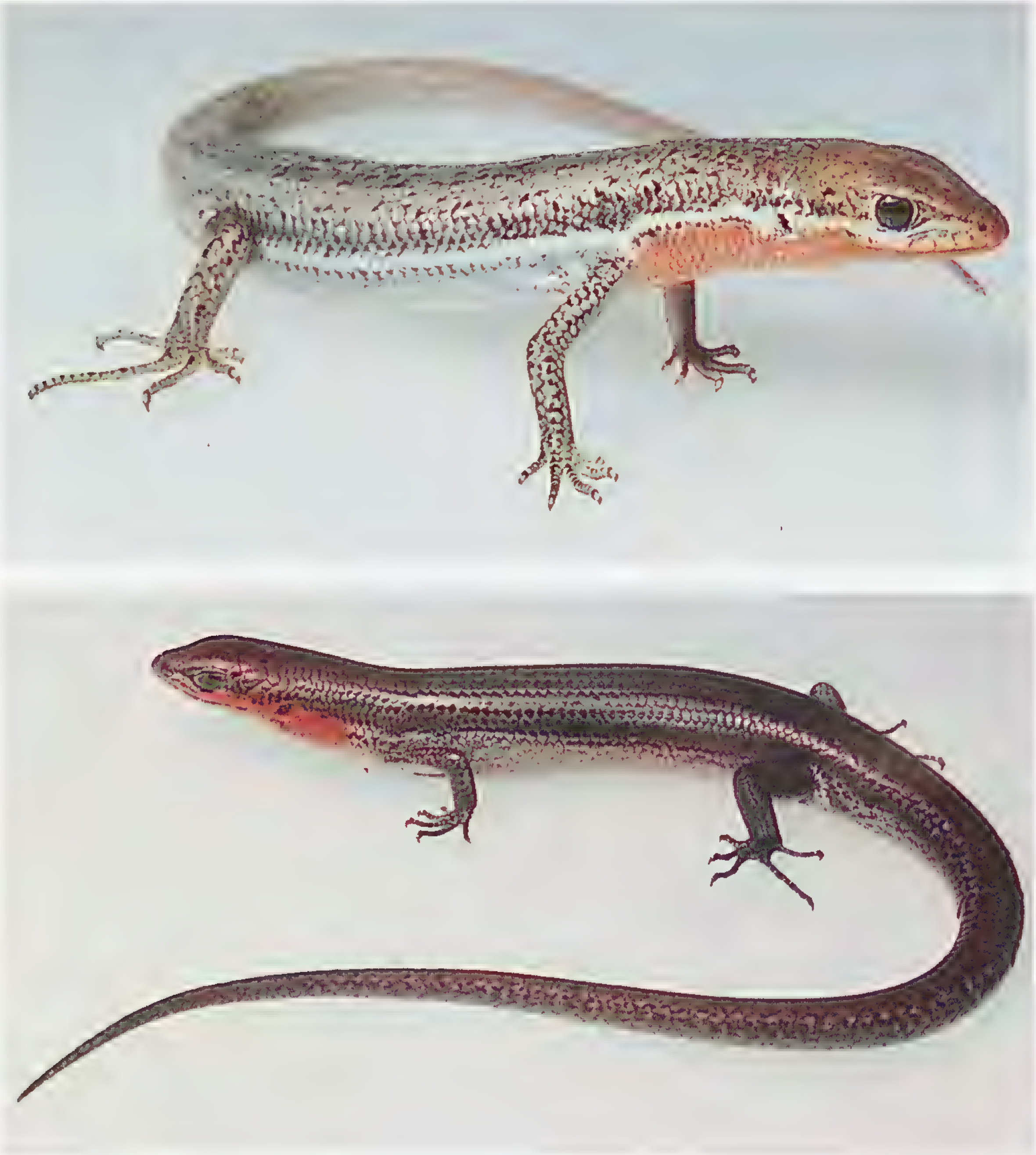

Fig. 4. Plate showing throat colour in an adult male *Morethia lineoocellata* from Rottnest Island, W.A. (top) and an adult male *Leiolopisma trilineatum* from Augusta, W.A. (bottom).

Within this subgroup, *Morethia* is most similar to *Cryptoblepharus* and *Proablepharus* in having an ablepharine eye. *Morethia* differs from *Proablepharus*, however, in having the frontoparietal and interparietal scales fused into a single scale instead of having all three scales distinct or the interparietal distinct from the fused frontoparietals. *Morethia* also usually has a distinct dark lateral stripe or area which *Proablepharus* lacks.

Most *Morethia* can be distinguished from most *Cryptoblepharus* by the presence of supranasal scales and by supraciliary scales which interdigitate with the supraocular scales rather than make linear contact with them. These convenient characters are not universal, however, in that some *Morethia* lack distinct supranasals (i.e., some *lineoocellata* and all *storri)* or have a linear contact between the supraciliaries and supraoculars (i.e., *butleri)* while some *Cryptoblerpharus* have distinct supranasals (e.g., some *africanus, eximius, poecilopleurus* and *novocaledonicus, fide* Mertens 1931 and pers. obs.).

*Morethia* and *Cryptoblepharus* can be readily distinguished from each other on the basis of a number of slightly more subtle but nonetheless significant characters. *Morethia,* for example, has a moderately deep head and body, a relatively long frontal scale, no enlarged upper periocular scales and, in most species, red colour in the tail during some stage of ontogeny, whereas *Cryptoblepharus* has a depressed head and body, a relatively short frontal, generally three large upper periocular scales, and no red in the tail.

## THE INTRAGENERIC RELATIONSHIPS OF *MORETHIA*

There are seven characters — five morphological and two colour — that are variable within *Morethia* and useful in inferring phylogenetic relationships within the genus. These seven characters are briefly analyzed below.

(A) EYE COVERING: All *Morethia* have an immovable clear spectacle permanently covering the eye, but in some species there is a distinct palpebral slit while in others the spectacle is completely fused to the underside of the supraocular shelf[1]. The palpebral slit is most logically viewed as an intermediate stage (A) in the evolution of the completely fused spectacle (a) and as such may be taken as the more primitive condition (Schwarz — Karsten 1933, Smith 1935 and 1937, Underwood 1970 and Greer 1974).

(B) SUPRANASAL SCALES. Most species of *Morethia* have the supranasals distinct from the nasals (B) whereas others have them fused to the nasals (b). The former condition appears to be primitive in lygosomines and the latter derived (Greer 1974).

(C) NUMBER AND RELATIVE SIZE OF SUPRACILIARY SCALES: The different species of *Morethia* have one of the following four character states: six relatively large supraciliaries (C), five large supraciliaries and a smaller sixth (c), five large supraciliaries only (c′), or four large supraciliaries and a very small fifth (c″). In that six relatively large supraciliaries is closest to the number seen in the more generally primitive members of the *Eugongylus* group, e.g., *Eugongylus, Leiolopisma spenceri*[2], *L. palfreymani* and an undescribed species of *Leiolopisma* from southwestern Australia, it is taken as the primitive condition and the lower numbers of large supraciliaries are taken as progressive reductions.

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[1] Rawlinson (1976:28) states that the "immoveable transparent disc (is) fused to the eye surface." This in incorrect; there is an easily probeable space (through the palpebral slit) between the disc and the surface of the eye.

[2] Rawlinson (1976:40) discounts my suggestion that *Leiolopisma spenceri* "would make a morphologically reasonable hypothetical ancestor" for the line leading to *Morethia* and its relatives (Greer 1974). His reason is that virtually all of the descendant taxa are oviparous whereas *Leiolopisma spenceri* is viviparous, and viviparity is clearly the more derived mode of reproduction. My own view of a taxon's morphology excludes its mode of reproduction, but I suppose a very broad view of morphology could include it. Be that as it may, the fact that viviparity in Australian skinks is so obviously an ecological phenomenon (Greer, in prep.) means that viviparity, even as a derived character, can count for little in phylogenetic inference. With this in mind, it does not seem unreasonable to speculate about a form morphologically similar to *Leiolopisma spenceri* but with an oviparous mode of reproduction.

(D) DEGREE OF INTERDIGITATION BETWEEN SUPRACILIARY AND SUPRAOCULAR SCALES: A straight-edged line of contact between the supraciliary and supraocular scales is the rule in lygosomines and as far as I know the interdigitating contact seen in all *Morethia*, except *butleri*, is unique within the *Eugongylus* group. For this reason, I take the straight-edged contact as the primitive condition (D) and the projection of the supraciliaries behind the first (d), first and second (d′), and first, second and third (d″) supraoculars as progressive derivations.

(E) SUBDIGITAL LAMELLAE: Most species of *Morethia* have smooth or only bluntly keeled subdigital lamellae, and as this is the condition seen in the more primitive members of the *Eugongylus* group, e.g., *Eugongylus* and *Leiolopisma*, it is taken as primitive (E) while the more unusual sharply keeled lamellae seen in only two species of *Morethia* is taken as derived (e).

(F) VENTRAL COLOUR: Ventral colour on the head and body is present in most of the species of the more primitive genera in the *Eugongylus* subgroup, e.g., *Eugongylus* and *Leiolopisma*[1]. This indicates that the presence of ventral colour is probably primitive in the subgroup as a whole and its absence derived.

The most primitive ventral colour pattern in *Morethia* is probably the extensive reddish-orange wash that develops seasonally on the chin and throat in the males of most species of *Morethia* (see Notes section and Fig. 4). The reason for thinking this is that this is the only ventral colour pattern shared with other members of the *Eugongylus* subgroup, i.e., the *trilineatum* species group of *Leiolopisma* and perhaps also the genus *Proablepharus* (see below), and at least in certain characters, i.e., a movable lower eyelid in the *trilineatum* species group and distinct frontoparietals and interparietals in *Proablepharus*, these relatives are more primitive than *Morethia*. This means that these taxa may have had a common ancestor with red throat colour and that they inherited this colour pattern as a primitive trait from the ancestor (F)[2]. The fringing reddish-orange ventral colour of *adelaidensis* (see Notes section) is probably derived (f), as it is unique in the *Eugongylus* group, and as reasoned above, the absence of any ventral colour in *ruficauda* is derived (f′), probably independently from the primitive condition.

(G) TAIL COLOUR: Most species of *Morethia* have a bright red tail as hatchlings and then lose this colour as they grow. Three species, however, apparently never have tail colour (see Notes section). The fact that most of the more generally primitive members of the *Eugongylus* subgroup, e.g., *Eugongylus* and *Leiolopisma*, lack tail colour would suggest that this is the primitive character state. Opposed to this, however, is the fact that there is one genus in the *Eugongylus* subgroup — the Australian *Proablepharus* — which shares a red tail with *Morethia* but is more primitive in having the frontoparietals and interparietal distinct instead of fused into a single scale. This latter consideration raises the possibility that red tail colour in both *Morethia* and *Proablepharus* was inherited from a common ancestor and is therefore primitive in both genera (G) and that the absence of red tail colour in *Morethia* is secondarily derived (g). It is difficult to decide which of these

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[1] Note, however, that ventral colour is apparently lacking in the very primitive *L. spenceri* (Rawlinson 1974 and pers. obs.).

[2] The fact that red throat colour occurs in both sexes and all age groups in the *trilineatum* species group (Rounsevell 1978 and pers. obs.) but only in adult male *Morethia* makes little difference to the phylogenetic analysis. Red throat colour in males is the common feature in both taxa and hence almost certainly characterized their hypothetical common ancestor.

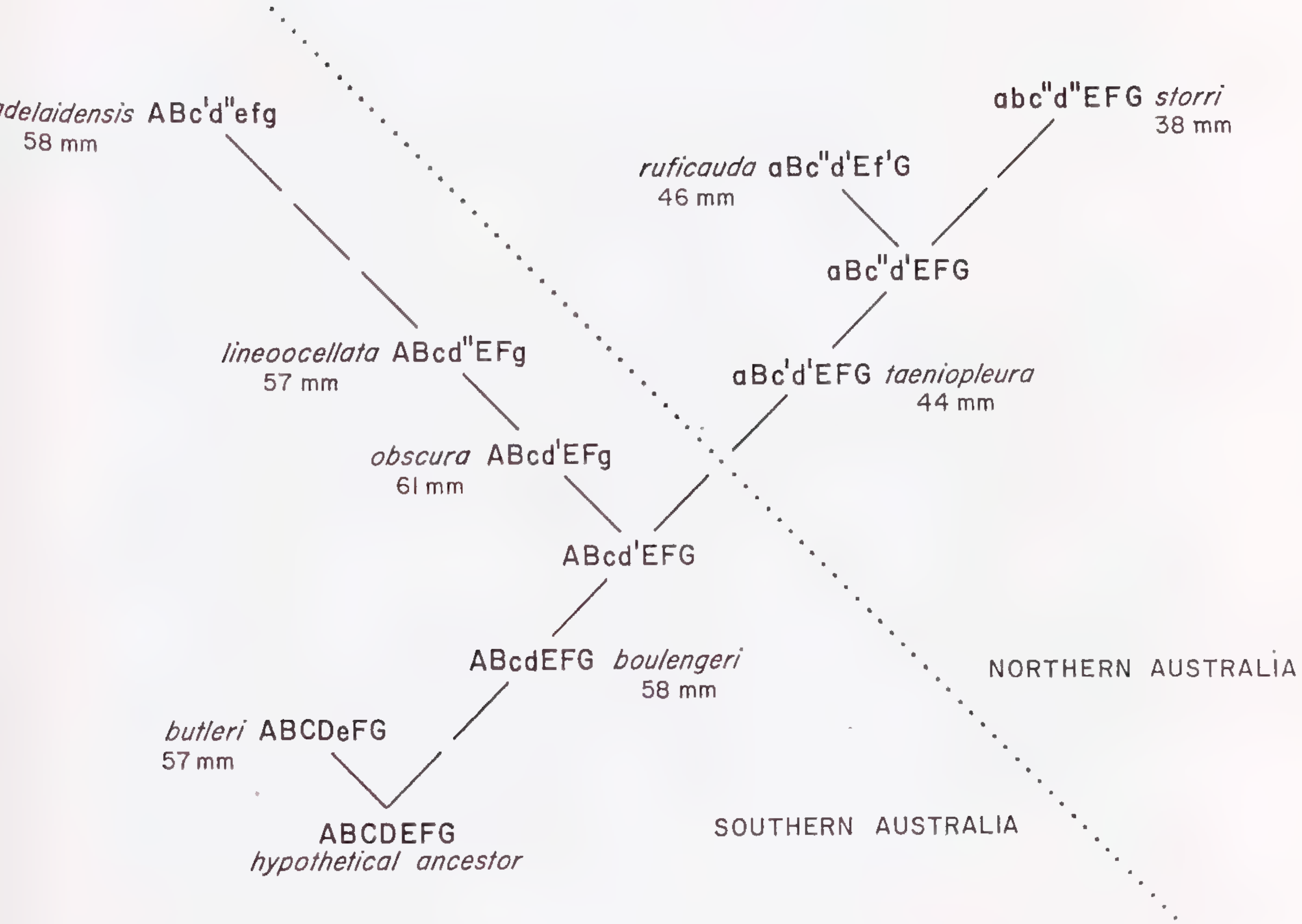

Fig. 5. A schematic representation of the inferred relationships of the eight living species of *Morethia* as determined from an analysis of seven characters (for which, see text) represented by letters A-G. In those cases in which a character state is variable within a species, the more primitive state is taken to represent the species. The distance between each taxon in the diagram is proportional to the number of character state changes separating it from its nearest relatives. The number below the name of each species is the maximum known snout-vent length (mm) for the species.

two possibilities is correct, but I prefer the second.

Utilizing the seven characters discussed above, it is possible to construct a phylogeny that is maximally parsimonious in that it hypothesizes no retrogressive events and only three convergent events. These are (1) the loss of the small sixth supraocular from a condition of five large supraoculars and a smaller sixth in two lineages, (2) the projection of the supraciliaries behind the third supraocular from a condition in which the supraciliaries project behind the first two supraoculars in two lineages, and (3) the acquisition of sharply keeled subdigital lamellae in two lineages (Fig. 5).

There are two interesting points in this phylogeny that are worth discussing briefly. First, there appear to be two distinct subgroups within *Morethia* based on morphology, colour pattern and distribution. The first, which comprises *adelaidensis, boulengeri, butleri, lineoocellata* and *obscura*, is characterized by an incompletely fused spectacle, relatively large body size (maximum SVLs from 57 to 61 mm) and a colour pattern featuring an ocellated, variegated or blotched mid-dorsal area, usually no distinct light dorsolateral stripe and usually a somewhat indistinct dark lateral stripe or area. This group is southern and temperate in distribution (Figs 6-8). The second group comprises *ruficauda, storri* and *taeniopleura* and is characterized by a completely fused spectacle, relatively small body size (maximum SVLs from 38 to 46 mm), and a colour pattern featuring a relatively patternless mid-dorsal area (the striking light mid-dorsal stripe of *ruficauda exquisita* is an exception but different from the pattern in the first group), a distinct light dorsolateral stripe and a distinct dark lateral stripe. This group is northern and tropical in distribution (Fig. 9). It may be noted here that Rawlinson (1976) has also suggested that the genus can be broken into two "geographical and evolutionary groups" along the same lines as suggested in this analysis, but he has given no reasons other than geography.

The second interesting point related to the phylogeny presented here is that the three most primitive species in the genus, i.e., *boulengeri, butleri* and *obscura*, are centred over temperate woodland and shrubland habitats (see Notes section below) — a fact which suggests that these habitats may be primitive for the genus. If this is true, *lineoocellata* can be viewed as occupying, at least over much of its range, the same kind of habitats, whereas *adelaidensis* and the northern group can be interpreted as having shifted into habitats that differ markedly either in structure, e.g., *adelaidensis*' low, halophytic (chenopod) shrubland, or in climate, e.g., the northern group's tropical distribution.

## THE BIOLOGY OF THE PRIMITIVE *MORETHIA*

Before proceeding to an analysis of *Morethia's* intergeneric relationships, it will be useful to review various aspects of the biology of the common ancestor of all living *Morethia*. It is this ancestor that is of interest in trying to determine *Morethia's* relatives. On the basis of the analysis in the preceding section and taking into account certain features found in all living *Morethia*, it seems likely that the primitive *Morethia* had the following morphology: supranasal present and distinct from nasal; lower eyelid with a clear window and fixed in the up position but not completely fused to the underside of the supraocular shelf; six subequally-sized supraciliary scales in linear contact with the supraoculars; frontoparietals and interparietal fused into a single scale; subdigital lamellae smooth or only bluntly keeled; chin and throat of adult males bright reddish-orange, at least seasonally; tail bright red, at least in the young, and a dark lateral stripe or area bordered below by a light stripe.

It is also probable that, like all living species, the primitive *Morethia* was both terrestrial and diurnal, and that it was oviparous with a variable number of eggs per clutch (see Notes section below). It also seems likely on the basis of the habitats occupied by the three most primitive species in the genus that the primitive *Morethia* occupied a temperate woodland or shrubland habitat (see above).

## THE INTERGENERIC RELATIONSHIPS OF *MORETHIA*

*Morethia* is clearly a member of the *Eugongylus* subgroup (Greer, 1979 and above), and the search for its relatives can be made with reference to both the characters and the taxa of this subgroup. The most reliable basis for inferring relationships is shared derived character states, and *Morethia* displays four character states which current knowledge suggests are either almost certainly or very likely to be derived within the *Eugongylus* subgroup. These are the fused frontoparietal and interparietal scales (Greer 1974 and 1977), a spectacle (see above), red throat colour, and red tail colour. These last two character states are presumed to be derived in the *Eugongylus* subgroup due to their restricted taxonomic occurrence. In the following discussion I compare *Morethia* with each of the genera in the *Eugongylus* subgroup using these derived character states. I also introduce certain other morphological characters, as well as data on ecology and distribution, in order to corroborate the evidence of the derived character states.

*Eugongylus* comprises three species which are centred over the islands of the southwest Pacific. It is the most generally primitive genus in the subgroup (Greer 1974) and shares no derived character states with *Morethia*. In fact, in the case of the two morphological characters of interest, each of which has three sequential states, *Eugongylus* shows the most primitive condition (frontoparietals and interparietal distinct and lower eyelid movable and scaly) whereas *Morethia* shows the characters in their most derived condition (frontoparietals and interparietal fused and the lower eyelid a spectacle). *Eugongylus* also differs greatly from *Morethia* in size; the maximum snout-vent length of the smallest species of *Eugongylus*, for example, is 162 mm (*mentovaria*, *fide* an unpublished MS by F.A.C.B. Adema) whereas the maximum SVL of the largest *Morethia* is only 61 mm. The two genera also differ in ecology and distribution. *Eugongylus* is a shade-dwelling to crepuscular inhabitant of mesic habitats (Messrs F. Parker and M. McCoy, pers. comms) on islands in the tropical Pacific whereas *Morethia* is a diurnal inhabitant of arid and semi-arid, continental Australia. These differences suggest that the relationship between *Eugongylus* and *Morethia* is not close.

*Phoboscincus* (two species) and *Tachygyia* (one species) appear to be independent derivatives of *Eugongylus* in the New Caledonian-Loyalty Islands Archipelago and the Tonga Islands, respectively (Greer 1974 and Böhme 1976). Both genera have fused frontoparietals and hence are one derived character state closer to *Morethia*[1] than is *Eugongylus*, but they differ from *Morethia* in the same way that *Eugongylus* does in all other morphological characters discussed, including size. Nothing is known of the ecology of either genus, as both are extremely rare, but *Phoboscincus* has pointed, recurved teeth which suggests that it has unusual feeding habits. The remote oceanic island distribution of the two genera, but especially the Tongan *Tachygyia*, is a further point of contrast with *Morethia* and may be taken, along with the other evidence, to indicate that neither genus is particularly closely related to *Morethia*.

[1] This is assuming that the fused frontoparietal and interparietal scales of *Morethia* were reached via an intermediate stage in which the frontoparietals were fused and the interparietal distinct and that this intermediate stage occurred in an immediate ancestor of *Morethia* (see below).

Böhme (1976) has recently described a new species of skink from New Caledonia and placed it in the genus *Eugongylus* along with *Phoboscincus* and *Tachygyia*. I believe that this species is rightly allied with *Eugongylus, Phoboscincus* and *Tachygyia*, but I also think that along with these other taxa, it merits separate generic rank. Be that as it may, the new species differs from *Morethia* in all the ways that *Eugongylus* does, plus others such as the absence of supranasals. It also probably has an even more distinctive ecology since the two known specimens were found inside a rotting log in moist rainforest. There is, therefore, nothing in the biology of this species that would indicate that it is closely related to *Morethia*.

*Anotis* comprises five species: two in Australia and three in New Caledonia (Greer 1974). The genus is slightly more plausible as a possible close relative of *Morethia* than any of the preceding taxa in that it shares fused frontoparietals (in one species), small size and an Australian distribution. Opposed to this, however, is the fact that *Anotis* shares no other derived character states with *Morethia* and the one species that does have fused frontoparietals is New Caledonian and not Australian. The genus is also highly cryptozoic and mesic adapted, to judge from the better known Australian species, and hence is quite distinct from the surface dwelling, xeric adapted *Morethia*. There seems to be little reason, therefore, to accept the notion that *Anotis* and *Morethia* might be close relatives.

In an earlier paper (Greer 1974), I suggested that *Morethia* was perhaps most closely related to the *Emoia-Cryptoblepharus* line and that it was possibly even derived from a *Cryptoblepharus*-like ancestor. When I made these suggestions, I only knew the animals on the basis of preserved specimens and was ignorant of them as living organisms. In the intervening six years, however, I have had an opportunity of seeing many of the animals and their relatives alive, and I have also considered their morphology in greater detail. As a result, I now think that the relationship between *Morethia* and the *Emoia-Cryptoblepharus* line is not particularly close. The reasons for my changed views are, briefly, as follows.

My original reason for allying *Morethia* with the *Emoia-Cryptoblepharus* lineage was that both groups had supranasals and fused frontoparietals. This is not a particularly convincing reason, however, as the former character state is primitive (Greer 1974) and hence not useful for inferring relationships and the latter character state has evolved many times in skinks and hence, by itself, does not provide strong evidence of relationship.

Detailed comparisons between each of the two genera in the lineage and *Morethia* also make it difficult to accept the notion that either is particularly closely related to *Morethia*. *Emoia* (approximately 36 species), for example, shares only the one derived character state with *Morethia*, i.e., fused frontoparietals[1], and the two genera differ greatly in ecology and distribution. *Emoia* is a basically mesic adapted taxon with its centre of diversity, and hence probable area of origin, in the islands of the southwest Pacific whereas *Morethia* is a basically xeric adapted taxon that probably originated in temperate, continental Australia (see above).

In addition to fused frontoparietals, *Cryptoblepharus* (approximately 36 species) shares a spectacle with *Morethia* and both taxa are broadly sympatric over much of arid and semi-arid Australia. These similarities are intriguing, but they are counterbalanced, I think, by substantial differences in morphology, colour and ecology. *Cryptoblepharus*, for example, has a very depressed head and body, a relatively small frontal, virtually no chromatic colour, and is almost exclusively arboreal and saxicolous. In contrast, *Morethia*

[1] *Emoia ruficauda* from the Philippines is an exception in that it has a bright red tail like *Morethia*. Given the great geographical distance separating these two taxa, however, it is unlikely that they shared a common ancestor.

has a typically deep head and body, a relatively large frontal, red colour in both the throat (in males) and tail (at least in juveniles), and is almost exclusively terrestrial. Furthermore, despite the fact that the two genera are now broadly sympatric in Australia, *Cryptoblepharus* probably evolved in tropical and subtropical habitats (Greer 1974) whereas *Morethia* appears to have evolved in temperate habitats (see above).

*Leiolopisma* is a diverse group of approximately 42 species distributed from the Chatham Islands, New Zealand and New Caledonia west through southern Australia to Round Island just north of Mauritius. The *trilineatum* species group is one of the most distinctive subgroups in the genus and is characterised by a slightly elongate body, the absence of a distinct supranasal scale and red throat colour. The species group comprises two or three species and is restricted to Australia: *platynotum* in the south-east and *trilineatum* with disjunct populations, that may have reached species status, in the southwest and southeast (Cogger 1975 and Fig. 10, this paper).

The fact that the *trilineatum* species group shares red throat colour and fused frontoparietals with *Morethia* (Fig. 4) suggests that the two taxa may be closely related. This hypothesis is also supported by the fact that the species group is similar to *Morethia* in general size (maximum SVLs range from 69 to 80 mm), shape and colour pattern (all forms have a dark lateral stripe or area and in some *trilineatum* at least this is bordered below by a light lateral stripe). The group is also somewhat similar to *Morethia* in ecology and distribution in that it is diurnal, terrestrial and oviparous and narrowly overlaps or abuts the distribution of the two most primitive living species of *Morethia*, i.e., *butleri* and *boulengeri* (compare Figs 6 and 10).

*Proablepharus*, the last genus in the *Eugongylus* group to be discussed, also appears to be closely related to *Morethia*. This genus occurs throughout most of mainland Australia and comprises three species: *reginae* in the west, *kinghorni* in the east and *tenuis* in the far north (Storr 1975, Cogger 1975 and Fig. 11, this paper).

*Proablepharus* is similar to *Morethia* in having a spectacle (which is incompletely fused), red tail colour at least in juveniles[1], and some reddish-orange colour on the head[2]. It is also similar in having the same general size (maximum SVLs range from 32 to 47 mm) and shape. Furthermore, *Proablepharus* is extremely similar to *Morethia* in ecology and distribution. It is diurnal, terrestrial and oviparous (known for *reginae* and *tenuis* — Mr B. Bradshaw and pers. obs., respectively) and is widespread in the arid and semi-arid parts of Australia (Fig. 11).

[1] *Proablepharus reginae* has bright red tail colour in hatchlings but loses this colour with age (Mr B. Bradshaw, pers. comm.). *P. kinghorni* has bright red tail colour in small individuals and the colour largely persists in larger individuals (pers. obs.). *P. tenuis* has a dull red wash on the tail in small individuals but this appears to be lost in larger animals (pers. obs.).

[2] *P. reginae* has a reddish-orange wash along the side of the face and neck (Messrs B. Bradshaw and L. A. Smith, pers. comm.). *P. kinghorni* apparently has this colour confined to the snout and anterior labial area (colour transparencies taken by Mr H. F. W. Ehmann and pers. obs.). It should be emphasised that the head colour in *Morethia* also extends to both these regions, at least in certain species, e.g. *lineoocellata* (Fig. 4). *P. tenuis* has an orange suffusion on the head and nape which is most intense over the snout and supraciliaries (Mr R. Sadlier, pers. comm.).

Although the age and sexual distribution of the head colour in *Proablepharus* is unknown, the available evidence is not incompatible with the hypothesis that the colour is restricted to adult males. The only specimen of *P. reginae* which showed head colour and which has been sexed is a male (Mr L. A. Smith, pers. comm.). Of the six specimens of *P. kinghorni* for which there are colour notes, three are males (SVL = 35 mm or >), all with colour and three are females (SVL = 34 mm or >), all without colour. The only specimen of *P. tenuis* noted to have head colour is a large male (SVL = 31 mm) with very enlarged testes.

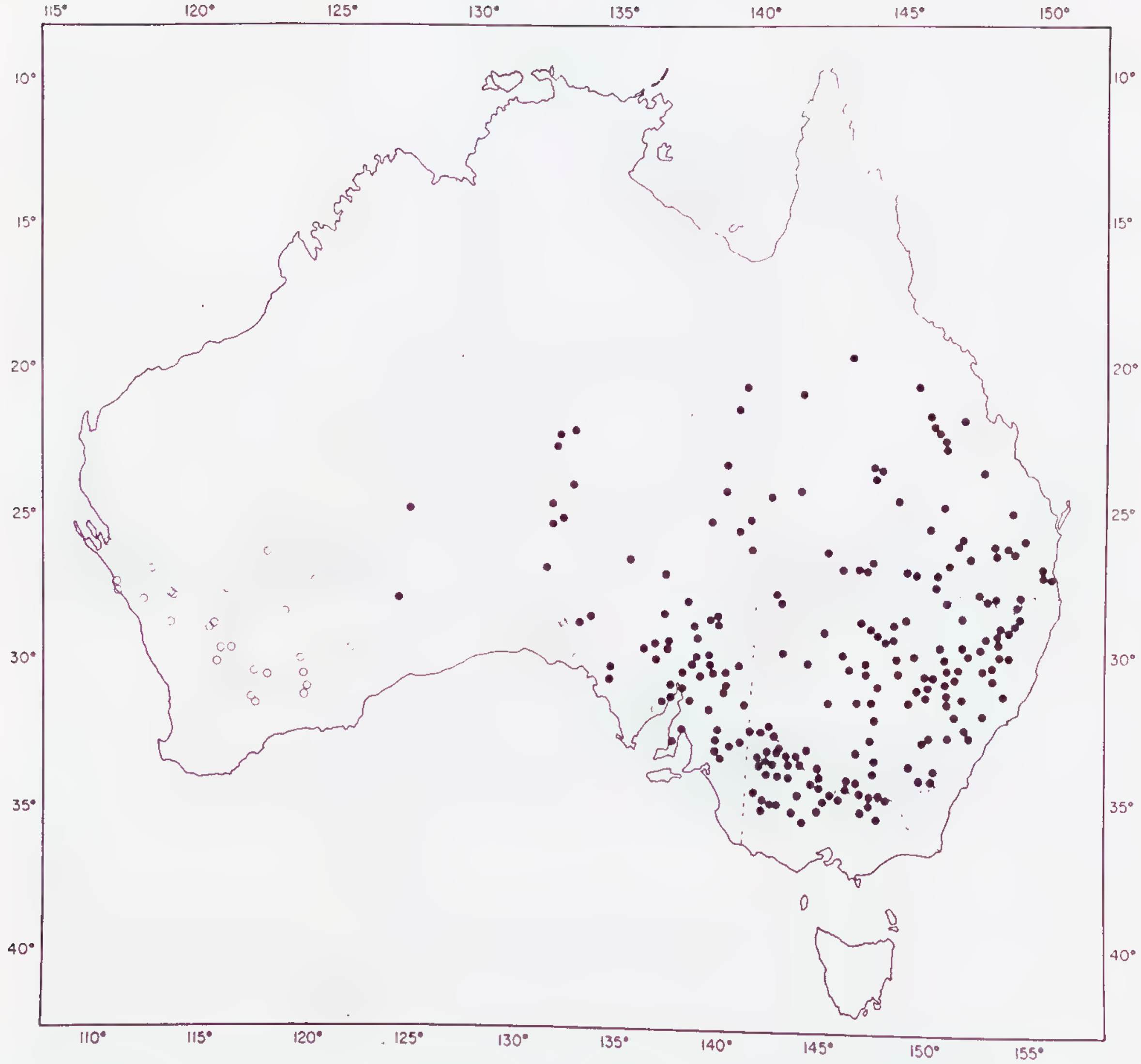

Fig. 6. Map showing the known distribution of *Morethia butleri* (open circles) and *M. boulengeri* (black dots).

Although the *trilineatum* species group and *Proablepharus* both appear to be fairly closely related to *Morethia,* I believe that the sum of the evidence actually favours *Proablepharus* as *Morethia's* closest living relative. The reason for this is that *Proablepharus* and *Morethia* share three derived character states and are broadly sympatric whereas the *trilineatum* species group and *Morethia* share only two derived character states and are only broadly parapatric.

If *Proablepharus* and *Morethia* are each other's closest living relatives, what can be said of their common ancestor? If one agrees that this ancestor can be "reconstructed" by combining the primitive character states unique to each taxon with the character states common to both, then the following picture emerges. Morphologically, this ancestor was a small skink with a distinct supranasal scale (inherited by *Morethia*), distinct frontoparietal and interparietal scales (inherited by *Proablepharus*), a spectacle, red tail, and some aspect of red throat colour (probably most like *Morethia* in its distribution for reasons that become apparent below). Ecologically, this ancestor was diurnal, terrestrial and oviparous and probably resident in a temperate, semi-arid habitat.

How is the *trilineatum* species group to be related to the *Morethia-Proablepharus* lineage? The most parsimonious hypothesis is that the two groups had a common ancestor which had a red throat at least in males (the only derived character state common to both groups), a distinct supranasal scale and distinct frontoparietal and interparietal scales (inherited by the ancestor of the *Morethia-Proablepharus* group), a movable lower eyelid with a clear window, and a dark-coloured tail (inherited by the *trilineatum* species group). In addition, this ancestor was probably diurnal, terrestrial, and oviparous and occupied a temperate, woodland habitat on the mesic periphery of a semi-arid area (features common to both groups).

If the relationships between *Morethia, Proablepharus* and the *trilineatum* species group are correct as described above (summarised in Fig. 12), then two cases of parallel evolution must be hypothesised. First, there is the independent loss of the supranasal scale in both *Proablepharus* and the *trilineatum* species group. It is unknown whether this loss in *Proablepharus* occurred by reduction or by fusion to the nasal, but in the *trilineatum* species group the loss has apparently occurred by fusion. The evidence for this is the bilateral presence in a single specimen of *platynotum* (AM R 39979) of a composite supranasal-postnasal that is partially set off from the nasal by fairly deep sutures. The second case of parallel evolution is the independent fusion of the frontoparietals in the line leading to *Morethia* on the one hand and to the *trilineatum* species group on the other. Independent evidence for the fusion of the frontoparietals within the *trilineatum* species group lineage is provided by the observation that in rare specimens the frontoparietals may be only partially fused (e.g., in the eastern form of *trilineatum* — AM 4705 and R 64715). It should also be mentioned that the phylogenetic relationships of these three taxa suggests that extensive red throat colour may have once occurred in the *Proablepharus* line but was reduced prior to the evolution of the living species in the genus.

The movable lower eyelid of the common ancestor of *Morethia, Proablepharus* and the *trilineatum* species group would have caused it to be identified as a species of *Leiolopisma* if it were alive today, and the supranasals and distinct frontoparietals and interparietal would have marked it as an extremely primitive species at that. In view of these facts, it is interesting to note that there are two species of *Leiolopisma* living in Australia today which show the structural characters just described: *L. spenceri* from southeastern Australia and an undescribed species from southwestern Australia known from only a single specimen (Western Australian Museum R 44969; Greer, in prep.). As alluded to several times above, however, *L. spenceri* appears to differ from this hypothetical ancestor in several other aspects of its biology, *viz.*, it is arboreal and

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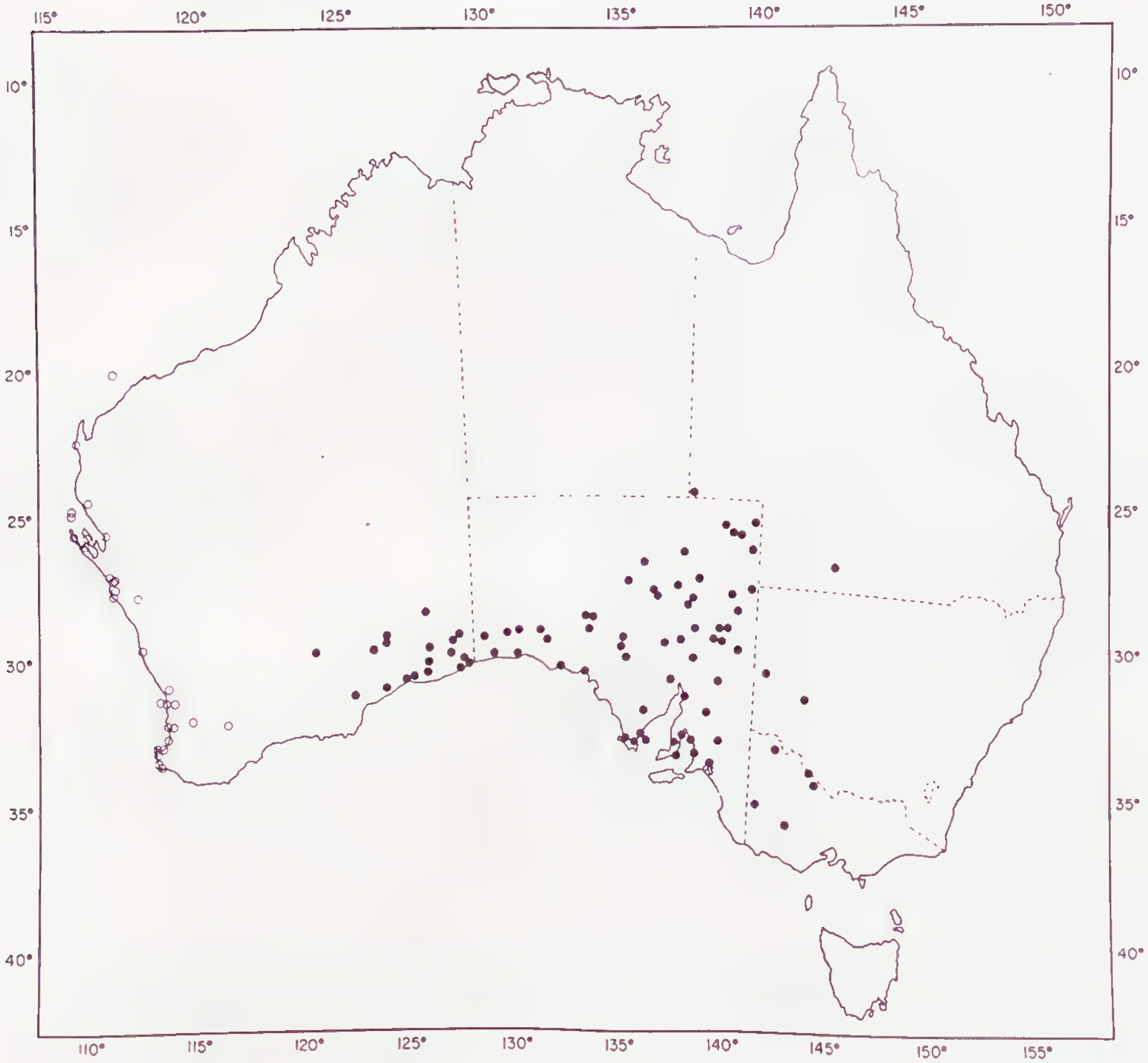

Fig. 7. Map showing the known distribution of *Morethia lineoocellata* (open circles) and *M. adelaidensis* (black dots).

saxicolous, live-bearing and lacks throat colour (Rawlinson 1974 and pers. obs.) whereas the common ancestor of *Morethia, Proablepharus* and the *trilineatum* species group was probably terrestrial, oviparous and had a red throat, at least in males. It is unfortunate that nothing is known of the biology of the undescribed species, except that the single known specimen was found on the ground; needless to say, it would be interesting to know the mode of reproduction and colour pattern in this species.

## A KEY TO THE SPECIES AND SUBSPECIES OF *MORETHIA*

(1.) A distinct brown to black lateral stripe bordered above by a very distinct white dorsolateral stripe; no palpebral slit; maximum snout-vent length = 46 mm; northern Australia .......... 2

A dark lateral stripe of varying distinctness bordered above by at best an indistinct white dorsolateral stripe or area; a distinct palpebral slit; maximum snout-vent length of smallest species = 57 mm; southern Australia .......... 5

(2) Supranasal distinct from nasal; supraciliaries project behind first and second supraoculars only .......... 3

Supranasal fused anteriorly to nasal; supraciliaries project behind first, second and third supraoculars ..........*storri*

(3) Four large supraciliaries and a smaller fifth that might be taken for a postocular; dorsolateral light stripe broad, separated from its fellow by three to five scale rows .......... 4

Five large supraciliaries; dorsolateral light stripe narrow, separated from its fellow by six scale rows ..........*taeniopleura*

(4) A distinct light mid-dorsal stripe..........*ruficauda exquisita*

No light mid-dorsal stripe ..........*ruficauda ruficauda*

(5) Supraciliaries project behind at least one supraocular, resulting in a zig-zag border between the supraciliaries and supraoculars.......... 6

Supraciliaries do not project behind any supraocular, therefore there is a straight border between the supraciliaries and supraoculars ..........*butleri*

(6) Supraciliaries project behind more than the first supraocular.......... 7

Supraciliaries project behind the first supraocular only ..........*boulengeri*

(7) Supraciliaries project behind the first, second and third supraoculars .......... 8

Supraciliaries project behind the first and second supraoculars only ......*obscura*

(8) Supranasal often fused to nasal anteriorly; five large supraciliaries plus a smaller sixth; toe lamellae smooth or obtusely keeled; ventral colour consists of a bright reddish-orange restricted to the throat of breeding males ..........*lineoocellata*

Supranasal distinct from nasal; five large supraciliaries; toe lamellae sharply keeled; ventral colour consists of a continuous reddish-orange fringe to the throat, chest and belly of breeding males ..........*adelaidensis*

## NOTES ON THE BIOLOGY OF *MORETHIA*

The preceding discussion of the intra and intergeneric relationships of *Morethia* introduced certain observations on the colour, reproduction, behaviour, habitat and distribution of the genus that may be elaborated on here.

### Colour

In his revision of the South Australian species of *Morethia* Smyth (1972) asserted that during the breeding season adult male *boulengeri* and *obscura* (his *lineoocellata*) develop a bright orange or orange-pink throat colour. He also noted that male *adelaidensis* in "breeding condition develop an orange colour all around the edges of the ventral surfaces, extending onto the inside surfaces of both fore and hind limbs and being particularly prominent around the vent and under the anterior part of the tail." In a later, more detailed study of *boulengeri* in an area just north of Adelaide, Smyth and Smith (1974) showed that the throat colour appeared in males in August and faded by mid-January and that changes in throat colour occurred in parallel with the testicular cycle.

My own observations support Smyth's observations on the location of ventral colour in male *Morethia* and indicate that male *butleri*, *lineoocellata* and *taeniopleura* are similar to *boulengeri* and *obscura* in having reddish-orange colour on the chin and throat. As noted above *storri* also has pinkish orange throat colour. It is also evident that in certain species, e.g. *lineoocellata,* the throat colour can extend up onto the snout and upper labials (Fig. 4).

In contrast, however, it seems as if *Morethia ruficauda* lacks ventral colour on the head and body. My own limited observations indicate that this is true and none of the people with whom I have spoken can recall having seen ventral colour on the head or body of this species (Dr H. G. Cogger, Mr M. Gillam, Mr G. F. Gow, Mr P. R. Rankin, Dr G. M. Storr and Mr R. Wells).

Previously published work (Smyth 1972, Storr 1972 and Rawlinson 1976) plus my own and other people's observations indicate that all species of *Morethia,* except probably *adelaidensis, lineoocellata* and *obscura,* have bright red tail colour, at least during the juvenile stages. Adult and hatching *adelaidensis* and *obscura* definitely lack red tail colour (pers. obs.). Adult *lineoocellata* also lack red tail colour (pers. obs.), and the late Mr P. R. Rankin, who had collected young *lineoocellata,* could find no indication in his field notes that these specimens had red colour in the tail, nor did the specimens themselves show any trace of it after having been in preservative for only a few months.

### Reproduction

Smyth and Smith (1974) provided a detailed analysis of the events in the reproductive cycle of *Morethia boulengeri* in an area north of Adelaide. Among other things, this study showed that the species is oviparous, with a clutch size ranging from 2-5 (mean = 3.7, N = 28) and that there was a positive correlation between clutch size and female size.

Rawlinson (1976) noted that *adelaidensis, boulengeri* and *obscura* are oviparous and that clutch sizes in *boulengeri* range from 3-5 (mean = 3.5, N = 11).

In an effort to learn more about the mode of reproduction and clutch size in *Morethia,* I examined all the state musuem collections plus my own collection (now in the Australian Museum) for females gravid with either enlarged, yolky ovarian eggs or oviducal eggs. For each gravid female I noted SVL and clutch size.

Females gravid with oviducal eggs were found for each of the eight species of *Morethia* and all had shelled eggs which appeared as if they would have been laid. Hence it may be concluded that the genus as a whole is oviparous.

There was a positive correlation between female size and clutch size within each species for which sample sizes were reasonably large (Table 2), and not surprisingly, there was also a positive correlation between mean size of gravid females and mean clutch size between species (r = .90, P < .01).

On 14 January 1979 I found a communal nest of *Morethia adelaidensis* on Reevesby Island in the Sir Joseph Banks Group off Eyre Peninsula, South Australia. The nest comprised 20 near term eggs plus one recently vacated shell. The eggs were partially buried in a crevice 8-12 cm beneath a granite boulder just above the high tide mark. If the mean clutch size for the species as a whole (3.2, Table 2) pertains to the Reevesby Island population, the nest could have represented the clutches of five to seven females. Some of the eggs hatched during collection and all had hatched by 24 January. None of the hatchings showed any sign of red throat or tail colour.

## Behaviour

There are relatively few observations in the literature on the behaviour of *Morethia*, and many of those that are available are of diminished value since they date from the time when all of the southern species were regarded as conspecific. The following is a brief review of what seems to be the more important published observations, supplemented with some personal observations.

Bustard (1968) reported that *boulengeri* (as *lineo-ocellatus anomalus* in his paper) "is a voracious feeder and will consume any insect which can be forced through its jaws", but he gives no data or observations. Bustard also reports that in northcentral New South Wales, the species has a "long active season and some bask throughout the winter."

Symth and Smith (1975) provided a fairly detailed analysis which showed that *boulengeri* "eats almost exclusively arthropods taken on the ground, and probably takes any animal of appropriate size it can catch."

Rawlinson (1976) described *boulengeri* as "heliothermic" and "insectivorous" but gave no details to support his assertion. He also said that this species has "high thermal preferences compared to other skinks from other temperate areas", but the other species he referred to are from obviously cooler habitats and hence the differences in thermal preferences are not surprising. Mr M. Gillam notes (in a letter of 10 January 1978) that *ruficauda* generally selects large exposed boulders for basking and that it is often active in high midday temperatures.

Smith (1976) reported that *ruficauda* "feeds by standing motionless in the open while curling its brilliant red tail horizontally back and forth as a lure." Due to the fact that these observations were obviously made in the presence of a potential predator, however, it is possible that what Smith has interpreted as feeding behaviour may have actually been some form of predator distraction behaviour.

All seven species with which I am familiar (all except *storri)* appear to be diurnal but generally crypotozoic during their activity period. The two northern species *ruficauda* and *taeniopleura* seem to be especially secretive, but this may simply be due to the fact that their small size causes them to be more easily overlooked.

*Morethia* is virtually completely terrestrial, but I have found *taeniopleura* a short distance above the ground in projecting portions of rotting timber.

Most species, perhaps all, sand swim quite readily, and will do so both as a means of escape and casual refuge. This sand swimming behaviour is especially interesting because it may provide a functional basis for the deep interdigitation of the supraocular and supraciliary scales seen in all species except *butleri*. This arrangement of the two parallel interlocking rows of scales may serve to resist the shearing forces induced by friction along the line of contact during forward motion under the surface.

### Habitat and Distribution

*Adelaidensis*. The general distribution of this species covers a large part of southcentral Australia (Fig. 7), but due to the fact that it is associated almost exclusively with chenopod shrubs, its distribution is likely to be as scattered and spotty as this plant community is itself.

*Adelaidensis* is apparently very tolerant of halophytic conditions. In South Australia, for example, I have found it beneath the first shrubs bordering the dry salt bed of Lake Everard, and Mr Glen Ingram tells me that in southwestern Queensland he has found it in the salt bush vegetation around salinas (see also Storr 1972).

The general distribution of *adelaidensis* (Fig. 7) broadly overlaps the distribution of *boulengeri* (Fig. 6) and *obscura* (Fig. 8), but I suspect that its close association with chenopod shrubs separates it locally from these species, both of which appear to prefer habitats with taller shrubs and trees (see below).

*Boulengeri*. This species occurs widely throughout the southeastern quarter of Australia (Fig. 6) in a variety of habitats ranging from open forest to medium height shrubland (Bustard 1968 and pers. obs.). In some of its habitats, such as the *Callitris* forests of northcentral New South Wales, it has been described as the "most common terrestrial skink" (Bustard 1968). Despite its wide geographical distribution and habitat diversity, however, the species rarely occurs near the coast, and it is unknown from any offshore island.

There are two problems with regard to the general distribution of *boulengeri* that merit mention. First, there is the problem of the three specimens in the Australian Museum (Palmer Register No. 4764 a-c) collected by Mr George Masters and registered as having come from "Port Lincoln", presumably at the tip of Eyre Peninsula in South Australia. Rawlinson (1976) accepted this record as valid, but I believe there are good reasons for questioning it. First, is the fact noted above that *boulengeri* rarely occurs at coastal localities. Second, no further specimens have been collected anywhere in the southern half of Eyre Peninsula (pers. obs. on all *boulengeri* in all Australian state museums), and Port Lincoln is in the far south end of the peninsula. And third, there is confusion with regard to at least two other localities involving Masters' specimens from southcentral South Australia: (1) the type of *Notechis ater* (Krefft 1866) was stated as having come from "Flinder's Range, South Australia" whereas the original register entry reads "Port Lincoln" and (2) the types of *Drysdalia masteri* (Krefft 1866) were registed as having come from "Flinder's Range" but this species, as it is currently understood, is not otherwise know from the Flinders Ranges (Mr H. F. W. Ehmann, pers. comm.).

The second problem with regard to the general distribution of *boulengeri* is that there are several areas in what could be considered the general distribution of the species, where, in fact, it is not known whether the species occurs or not. The two most important of these areas are the Simpson Desert and the Great Victoria Desert. Clearly our understanding of the species' habitat associations and its spatial relations with congeners could vary greatly depending on its distribution in these areas.

The distribution of *boulengeri* either overlaps or interdigitates with the distribution of five other species of *Morethia*. In the northeast and northwest *boulengeri* overlaps narrowly with *taeniopleura* and *ruficauda*, respectively, and in the far west and southwest it narrowly overlaps or interdigitates with *butleri*. In none of these cases, however, is the nature of the habitat separation between the species known.

*Boulengeri* appears to occur in fairly broad sympatry with *adelaidensis* and *obscura* in parts of southeastern South Australia, southwestern New South Wales, and northwestern Victoria. I know of no instance, however, where even two of the species have been found together in an area of uniform habitat. This is no doubt due to the fact that the general habitat associations of the three species are somewhat different (pers. obs.). *Boulengeri*, for example, appears to be closely associated with relatively heavily wooded habitats such as brigalow and dense shrubland, whereas *obscura* seems to occur in more open shrub habitats such as mallee, and *adelaidensis* is largely associated with open, low shrub habitats such as chenopod communities.

*Butleri*. Based on current information, this species appears to occur in two disjunct areas: the largely interior parts of the southern third of Western Australia, and the central part of southern South Australia (Fig. 6)[1]. It is uncertain, however, whether this disjunction is real or not. In my experience *butleri* appears to be strongly associated with woodland and tall shrub habitats and is generally absent from open low shrub habitats (see also Pianka 1969). It is possible therefore that while the species is absent from the more or less accessible parts of the intervening Nullarbor Plain, it is continuously distributed in the relatively inaccessible mallee belt north of the Plain.

It is also uncertain how the distributions of *butleri* and *boulengeri* relate to each other. On the very broadest scale, they would appear to overlap widely, but they may, in fact, interdigitate or form a mosaic. Either of these latter possibilities would not be surprising as the two species appear to be morphologically and ecologically similar (Storr 1972).

The only species with which *butleri* does broadly overlap is *obscura*. I have collected both species at a locality just south of Norseman, Western Australia, in a woodland of medium height and little ground cover, but I formed no impression of any microhabitat differences.

*Lineoocellata*. The distribution of this species is largely centred over the coastal plain of midwestern and southwestern Western Australia (Fig. 7) (Storr 1972). The few inland populations are presumably relict.

Despite the species' restricted geographical distribution, it seems to have a fairly broad habitat range. On Rottnest Island, for example, I have seen it on the samphire flats bordering the salt lakes just behind the main settlement, and in the vicinity of Busselton, I have collected it both on sparsely vegetated dunes and in heavily wooded Tuart Forest. Elsewhere these habitats might have been typically occupied by *adelaidensis*, *obscura* and *boulengeri*, respectively.

An investigation of the habitats occupied by the isolated inland populations would be very interesting, especially with regard to how they may differ from any neighbouring habitats occupied by the closely related (Storr 1972) and widespread *obscura*.

*Obscura*. This species is widely distributed throughout southern Australia (Fig. 8), including most of the offshore islands.

In my experience, *obscura* is largely associated with open woodland and shrubland, although in certain areas such as along the south coast of Western Australia, it also occurs on the coastal plain (Storr 1972) in coastal heathland (pers. obs.).

1. Smyth (1972) assigned a specimen from Ooldea, South Australia to *butleri*, but noted that it differed slightly from Western Australian specimens in the squamation of the supraocular region. Perhaps for this reason, neither Smyth (1972) nor Rawlinson (1976) mapped *butleri* in South Australia. I have examined this Ooldea specimen and others subsequently acquired by the South Australian Museum and on this basis can confirm the presence of *butleri* in central-southern South Australia (Fig. 6).

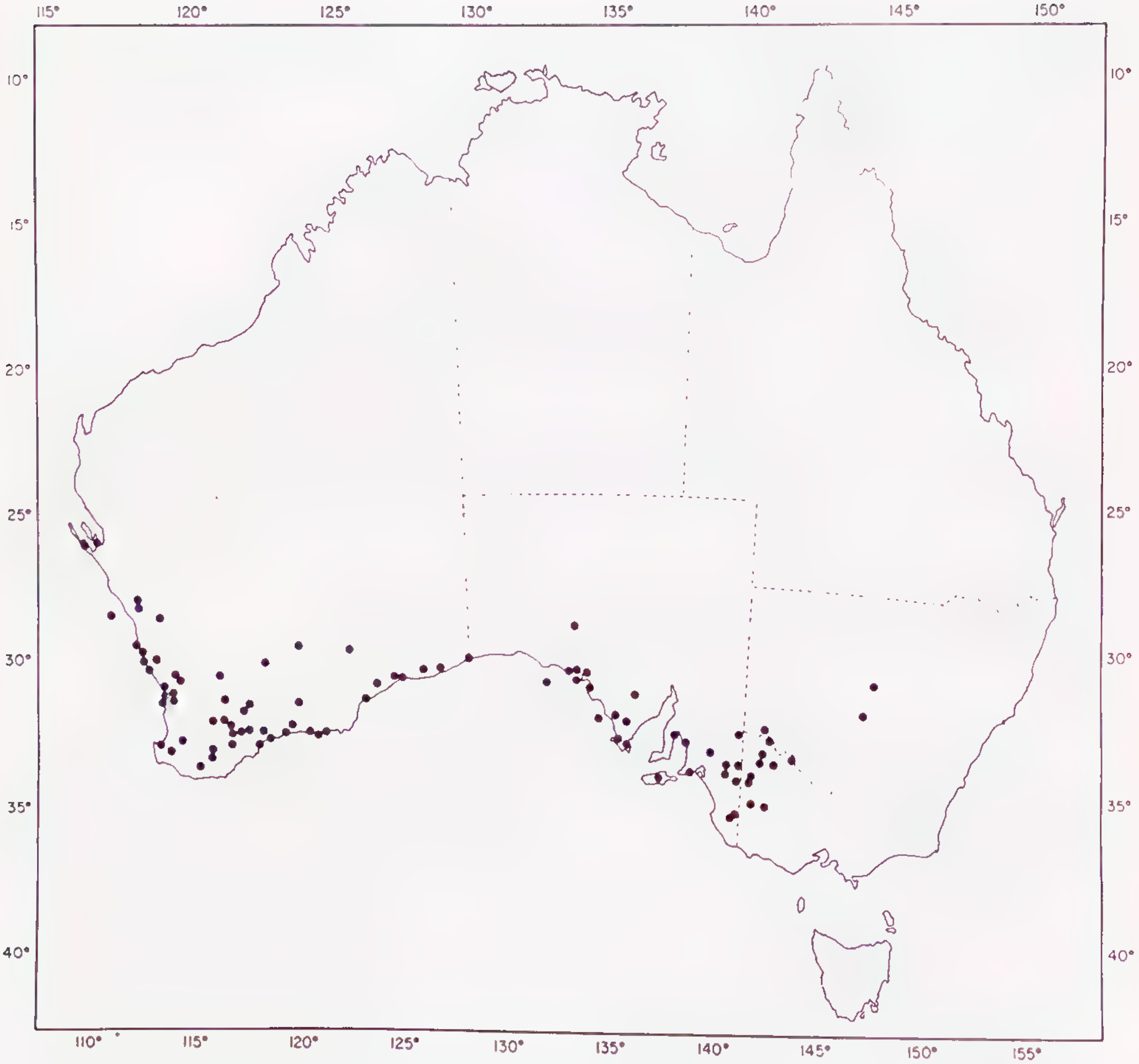

Fig. 8. Map showing the known distribution of *Morethia obscura*.

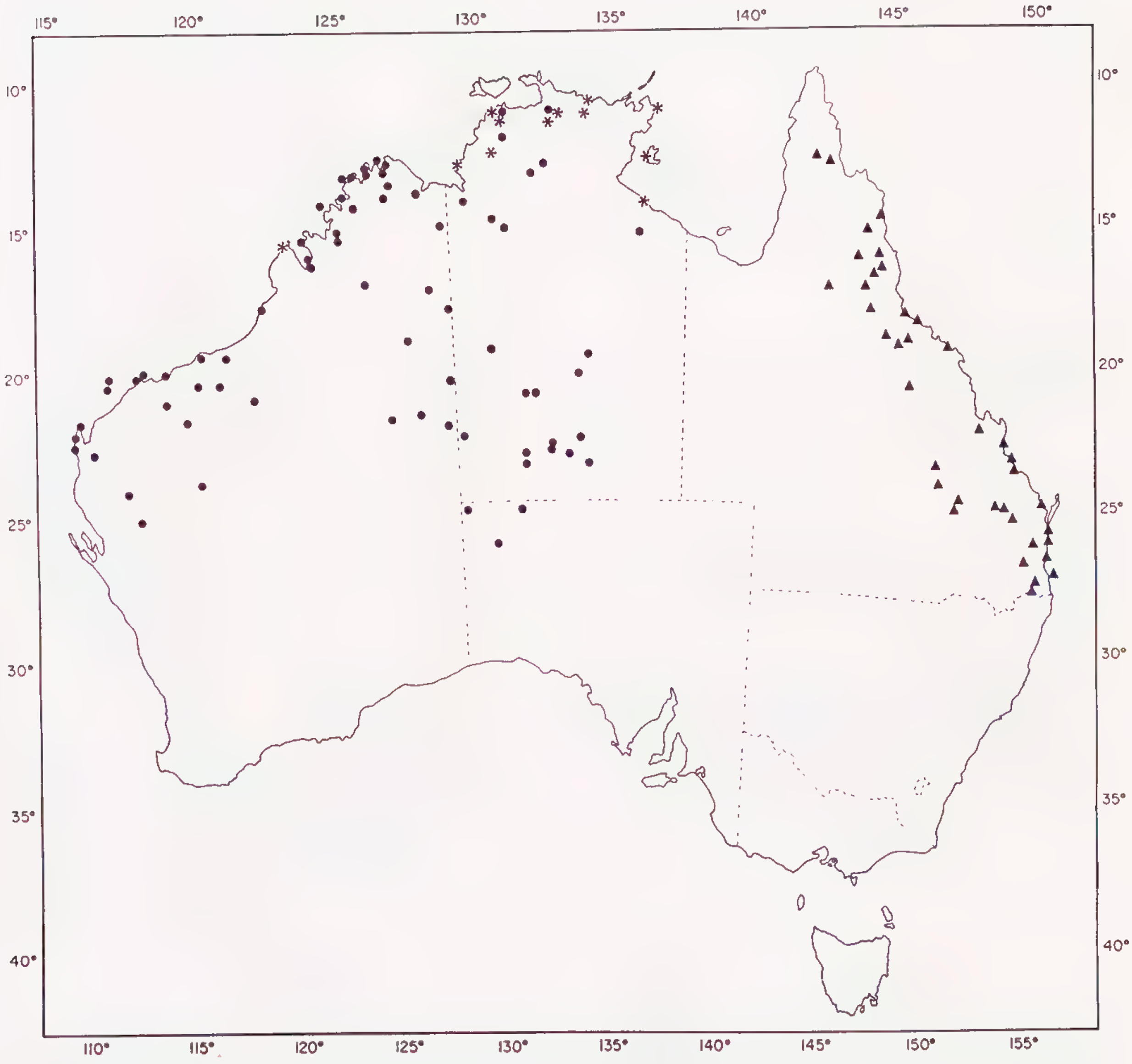

Fig. 9. Map showing the known distribution of *Morethia taeniopleura* (black triangles), *M. ruficauda* (black dots) and *M. storri* (asterisks).

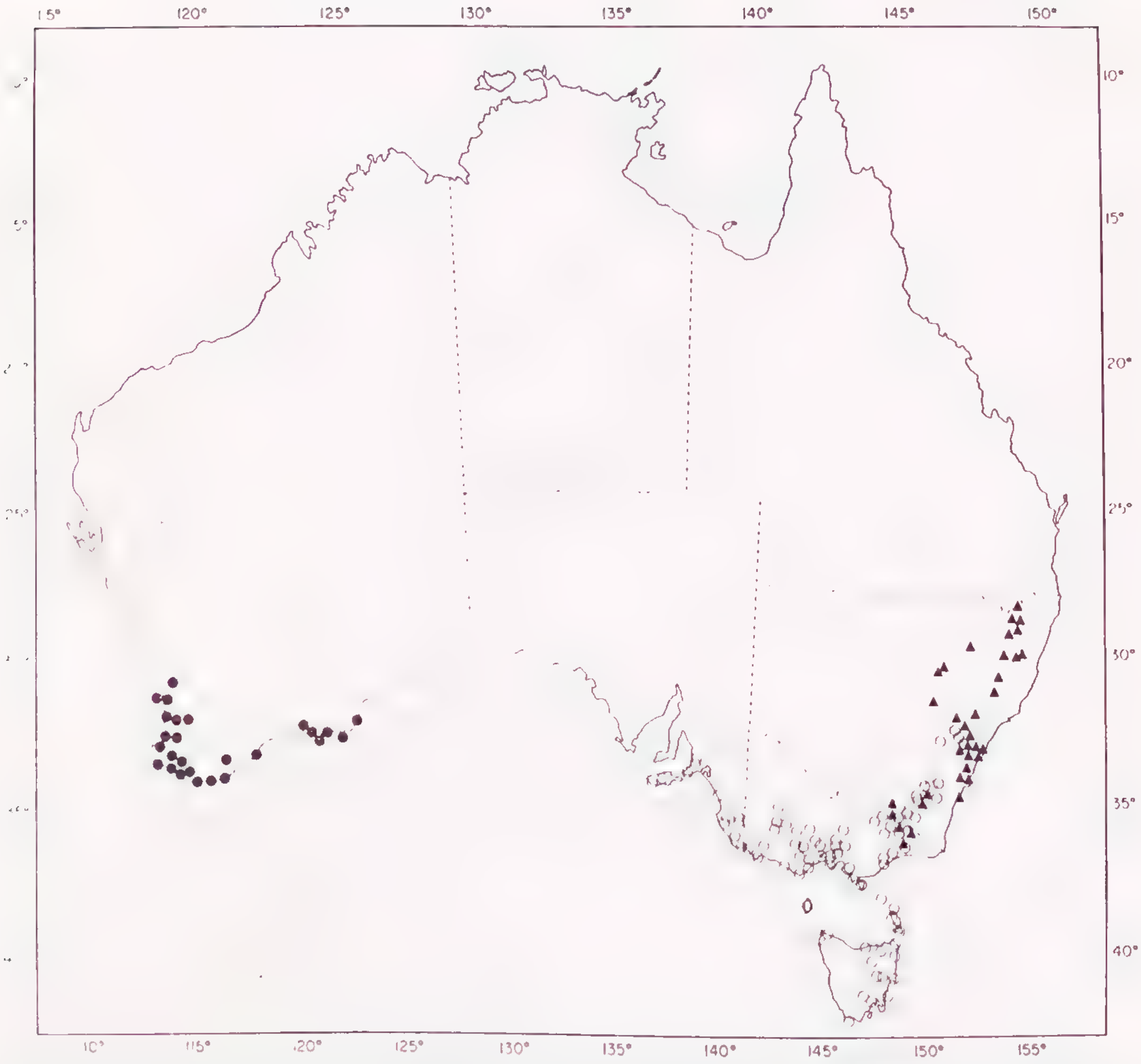

Fig. 10. The distribution of the three forms of the *trilineatum* species group of *Leiolopisma: platynotum* (black triangles) and the eastern (open circles) and western (black dots) forms of *trilineatum*.

The populations mapped in central New South Wales are interesting in that they are generally distinguishable from all other populations in being uniformly coloured above instead of ocellate. Rawlinson (1976) has mapped these populations as being continuous with the rest of the species' distribution, but they may, in fact, be isolated. The populations inhabit an eastern outlier of the mallee-*Triodia* association (Dr H. G. Cogger, pers. comm.) which is more extensive to the southwest and which may have retreated from central New South Wales after the last dry period of the last glacial some 25000-13000 years B.P. (Bowler 1976). This same habitat also supports a relict population of *Amphibolurus fordi* (Cogger 1974).

*Ruficauda*. This species is widespread over the northwestern quarter of Australia (Fig. 9), and its distribution covers some of the most arid parts of the continent. It has been found in a variety of habitats ranging from woodland to open grassy flats. It occurs on both rocky and hard-packed sand substrates but appears to avoid loose sand dunes (Mr M. Gillam pers. comm. and pers. obs. for subspecies *ruficauda*, but note that Smith [1976] records the subspecies *exquisita* from "all habitats but mostly siliceous foredunes and consolidated dunes" on Barrow Island).

In certain areas along the periphery of its distribution, *ruficauda* is broadly sympatric with three other species of *Morethia: boulengeri* in the southern part of the Northern Territory and perhaps the northwest corner of South Australia, *lineoocellata* in the northwest of Western Australia, and *storri* in the northern part of the Northern Territory. In none of these areas, however, is anything known about the habitat differences between the species.

It may be noted here that Pianka (1972) has suggested that this species (as *taeniopleura* in his paper) appeared to have isolates in the Central Ranges. Present information, however, indicates that the distribution of *ruficauda* in the Central Ranges is part of a continuous distribution to the north and west (Fig. 9).

*Storri*. This species is known at present from two disjunct areas in northern Australia: the near coastal regions of the northern part of the Northern Territory and Dampier Land in Western Australia (Fig. 9). This disjunction is almost certainly a collecting artifact, however, and additional field work will probably fill the gap. *Storri* appears to occur in a variety of habitats ranging from open woodland to open grassland (see species description above). It is broadly sympatric only with *ruficauda*, but the nature of the niche differences between the two species is little understood.

*Taeniopleura*. This species occurs in far eastern Queensland between the upper part of Cape York and the lower north slopes of the Macpherson Range (Fig. 9).

The species has been collected on the following islands: Magnetic, Curtis, Bribie and North Stradbroke. It has also apparently been seen but not collected on Fraser Island (Barry and Campbell 1977). There appear to be no records for any of the Whitsunday Islands, but this may be due to lack of collecting.

*Taeniopleura* occurs in fairly open and at least seasonally dry habitats ranging from large artificial grass clearings and wallum to open sclerophyll forests (pers. obs. and Covacevich and Ingram 1975). It has also been found associated with a semi-evergreen vine thicket (with *Brachychiton* emergent) in the Bunya Mountains (Covacevich 1977).

The range of *taeniopleura* overlaps that of *boulengeri* in southeastern Queensland, but there seems to be no information on how the habitat requirements of the two species differ in sympatry. I personally know of only one case of the two species having been found together at the same locality. This was around the rubbish tip at the Belyando Star

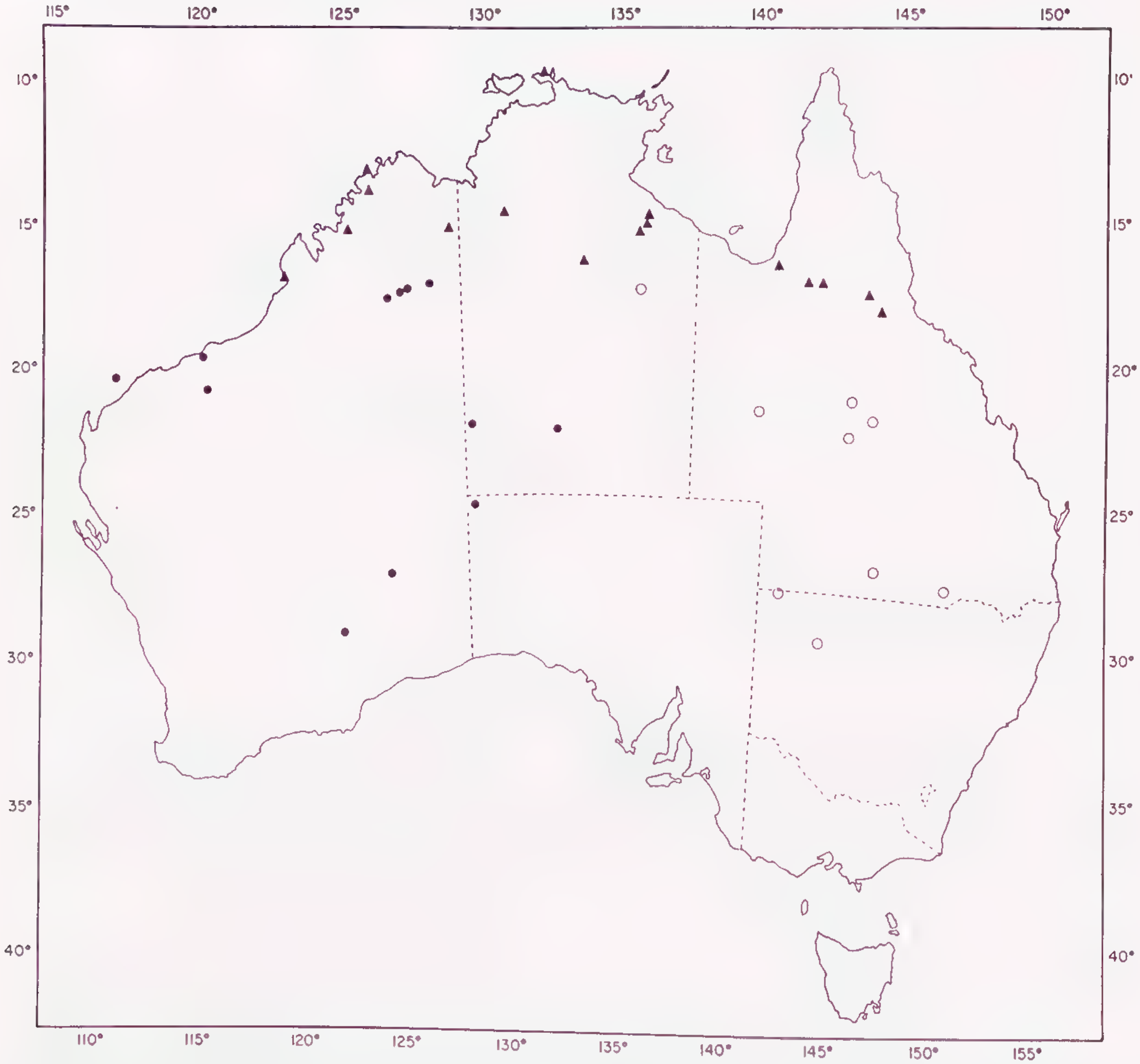

Fig. 11. The distribution of the three species of *Proablepharus: kinghorni* (open circles); *reginae* (black dots) and *tenuis* (black triangles).

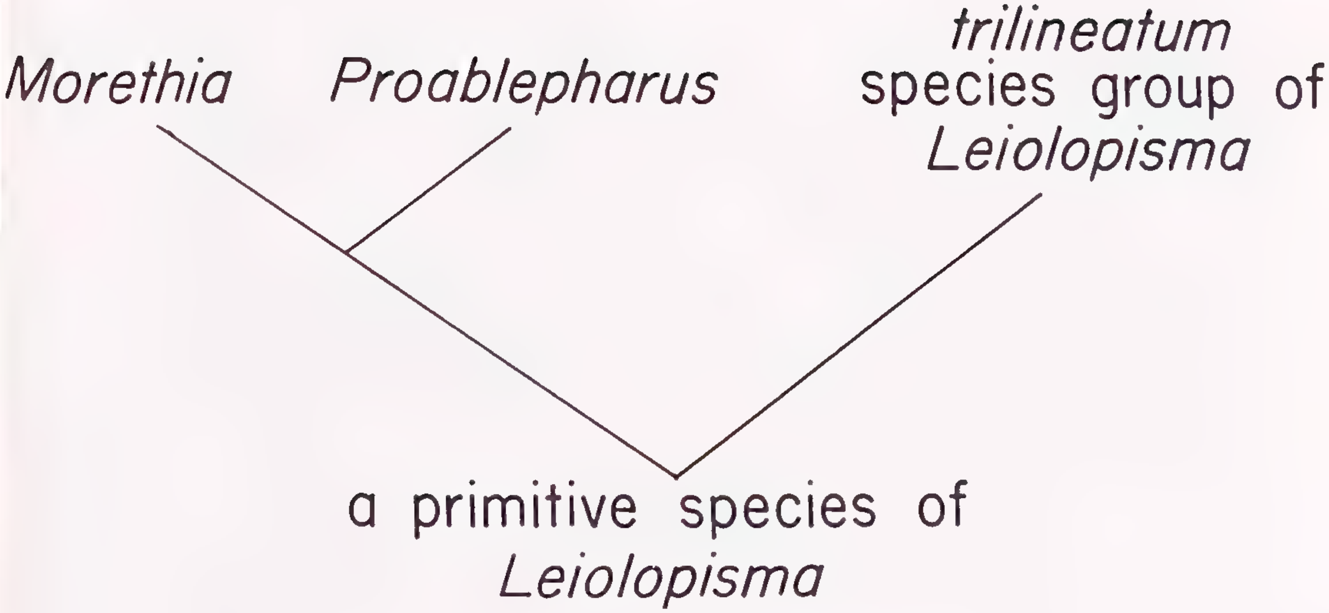
*Morethia*
*Proablepharus*
*trilineatum* species group of *Leiolopisma*
a primitive species of *Leiolopisma*

Fig. 12. A schematic representation of the phylogenetic relationship hypothesized for *Morethia*, *Proablepharus* and the *trilineatum* species group of *Leiolopisma*. See the text for the details and rationale.

Service Station on the Gregory Highway. The locality was in a grassy open forest and single specimens of each species were obtained during general collecting.

The long and relatively narrow, near coastal distribution of *taeniopleura* parallels that of *lineoocellata* in Western Australia, and if very near coastal populations of *taeniopleura* were chosen, the two species might provide some interesting comparisons of biogeographic trends.

## ACKNOWLEDGEMENTS

A number of people made substantial contributions to this paper by providing me with their field observations on various species of *Morethia* and *Proablepharus*. I would like to thank specifically the following for this very generous help: Mr B. Bradshaw, Dr H. G. Cogger, Mr H. F. W. Ehmann, Mr M. Gilliam, Mr G. F. Gow, Mr G. Ingram, Mr R. E. Johnstone, the late Mr P. R. Rankin, Mr R. Sadlier, Mr L. A. Smith, Dr G. M. Storr and Mr R. W. Wells.

I am grateful to Mr H. F. W. Ehmann for bringing to my attention the problems involved with some of George Masters' South Australian localities.

The following people also greatly aided the development of this paper by providing critical readings of the manuscript: Dr H. G. Cogger, Mr H. F. W. Ehmann, Ms P. K. Greer, the late Mr P. R. Rankin, Mr R. Sadlier and Dr G. M. Storr.

The photograph of *Morethia storri* in Fig. 2 was kindly provided by Dr H. G. Cogger and the illustrations for Figs 1, 3, 5 and 12 were executed by Ms P. K. Greer.

Finally, I would like to express my very great appreciation to the Australian-American Educational Foundation, Canberra, A.C.T. for providing the financial support which enabled me to study *Morethia* and other skinks both in the field and in various Australian museums.

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Manuscript accepted for publication 23 November, 1978.

**TABLE 1.** **A comparison of certain systematically important characters between** *Morethia storri* **new species and its two nearest relatives.**

| Character | *storri* | *taeniopleura* | *ruficauda* |
|---|---|---|---|
| Midbody scale rows | | | |
| Range | 24-28 | 24-29 | 24-27 |
| Mode | 26 | 26 | 26 |
| Mean | 26.2 | 26.2 | 26.4 |
| N | 18 | 42 | 34 |
| Paravertebral scales | | | |
| Range | 54-58 | 55-64 | 54-58 |
| Mean | 56.1 | 59.7 | 56.6 |
| S.D. | 1.44 | 2.29 | 1.68 |
| N | 14 | 30 | 12 |
| Subdigital lamellae (fourth toe) | | | |
| Range | 17-21 | 18-22 | 17-23 |
| Mean | 19.4 | 20.2 | 20.0 |
| S.D. | 1.05 | 1.33 | 1.72 |
| N | 20 | 55 | 37 |
| Supranasal fused anteriorly to nasal (+) or completely distinct (–) | + | – | – |
| Suparoculars bordered posteriorly by medially projecting supraciliaries | 1-2-3 | 1-2 | 1-2 |
| Supraciliaries | 4 large,<br>1 small | 5 large | 4 large,<br>1 small |
| Width of mid-dorsal area between light dorsolateral lines (in scale rows) | 6 | 6 | 3-5 |
| Dorsolateral light stripe extends to snout (S) or eye (E) | E | E | S |

| | | | |
|---|---|---|---|
| Snout-vent length (mm) | | | |
| Range | 17-38 | 18-42 | 20-46 |
| N | 20 | 51 | 182 |
| Length of foreleg/ snout-vent length | | | |
| Range | .25-.35 | .23-.29 | .23-.32 |
| N | 14 | 11 | 16 |
| Length of rear leg/ snout-vent length | | | |
| Range | .36-.47 | .33-.43 | .33-.46 |
| N | 14 | 11 | 16 |
| Tail length/ snout-vent length | | | |
| Range | 1.32-1.76 | 1.06-1.82 | 1.49-2.17 |
| N | 3 | 35 | 4 |

**TABLE 2. Data on certain reproductive parameters in gravid** *Morethia.*

| Parameter | *adelaidensis* | *boulengeri* | *butleri* | *lineoocellata* | *obscura* | *ruficauda* | *storri* | *taeniopleura* |
|---|---|---|---|---|---|---|---|---|
| SVL of gravid♀♀ (mm) | | | | | | | | |
| Range | 44-58 | 40-54 | 49-57 | 38-57 | 39-55 | 31-42 | 36-38 | 36-44 |
| Mean | 49.0 | 47.5 | 53.3 | 46.1 | 47.4 | 36.2 | 37.0 | 39.2 |
| N | 33 | 74 | 11 | 32 | 52 | 12 | 2 | 14 |
| Clutch size | | | | | | | | |
| Range | 2-6 | 1-6 | 2-5 | 2-5 | 1-5 | 1-3 | 2-3 | 2- 4 |
| Mean | 3.2 | 3.2 | 3.8 | 2.8 | 3.1 | 2.0 | 2.5 | 2.4 |
| N | 33 | 74 | 11 | 32 | 52 | 12 | 2 | 14 |
| Correlation coefficient of clutch size us SVL | .58 | .58 | .30 | .39 | .55 | .79 | — | .57 |
| | $P<.001$ | $P<.001$ | $P>.05$ | $P<.05$ | $P<.001$ | $P<.01$ | — | $P<.05$ |

# THE SWAIN REEFS EXPEDITION: OPHIUROIDEA

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## SUMMARY

Thirty species of ophiuroids collected at the Swain Reefs, north-east of the Capricorn Channel near the southern limit of the Great Barrier Reef are discussed. The ophiocomid genus *Ophiopsila* Forbes is newly recorded for Australian waters with the description of a new species. In addition, there are six new species records for Australia and a further two species are newly reported for the Great Barrier Reef itself. Extensive colour notes for the living brittlestars are reported together with new extensions of species' ranges.

## INTRODUCTION

The echinoderm fauna of the Great Barrier Reef has formed the focus of several expeditions (reviewed in Gibbs *et al.*, 1976). For the most part, the echinoderms of its northern region have been the most intensively documented (for example H. L. Clark, 1921, 1938, 1946; Gibbs *et al.*, 1976) but in comparison those of its southern region have been rather neglected. In 1962, the Swain Reefs, lying to the north-east of the Capricorn-Bunker group (21°43'S: 152°25'E), were surveyed and sampled by a party from The Australian Museum. The large and diverse collection of echinoderms obtained by the 1962 expedition was placed in The Australian Museum: the majority of the ophiuroid species presently reported are derived from that collection. The crinoids collected by the Swain Reefs Expedition have been described previously (A. M. Clark, 1975).

A total of thirty species, mostly representing ophiuroid genera commonly found in coral-reef environments, is recorded (A. M. Clark, 1976). The ophiocomid genus *Ophiopsila* Forbes is reported for the first time from Australian waters with the description of a new species, *Ophiopsila gilletti.* New records for Australian waters comprise: *Amphiura (Amphiura) luetkeni* Duncan; *Ophiomastix luetkeni* Pfeffer; *Ophionereis intermedia* A. M. Clark; *Ophiarachnella macracantha* H. L. Clark; and *Ophiodyscrita pacifica* Murakami. *Ophioconis cincta* (Brock) and *Amphioplus (Amphichilus) ochroleuca* (Brock) are newly recorded for the Great Barrier Reef. Of the remaining species reported, fourteen represent further southward extensions of their ranges from the northern part of the Great Barrier Reef.

An important feature of the Swain Reefs collection is the numerous colour notes and colour transparencies of the living brittlestars that accompany the preserved material. This has permitted a comparative study of the colouration of the living and preserved specimens to be made, a study that is particularly relevant to those ophiuroid taxa in which infrageneric diagnoses are made on the criterion of colour patterns (for example the family Ophiotrichidae). H. L. Clark frequently recorded the colour of live echinoderms and the colour changes associated with preservation, notably in his discussion of the Torres Strait fauna (H. L. Clark, 1921) with its accompanying lithographs. Where applicable, these data have been included in the systematic account for comparative purposes, as have the recent colour photographs of living, *in situ* ophiuroids presented by Coleman (1977).

For each species, the station and number of specimens are given; further details of the stations appear in Table 1. The prefix 'off Gillett Cay" refers to material collected prior

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to the main Swain Reefs Expedition of 1962. Further echinoderms were collected from the Swain Reefs in 1974 by Mr Neville Coleman, Marine Associate of The Australian Museum; these are identified by the prefix '1974'. J numbers refer to the registration numbers of specimens located in The Australian Museum's collection.

Kodachrome colour transparencies (taken by Anthony Healy, 9-126 Shirley Road, Crows Nest, Sydney, NSW 2065) are available for ten of the ophiuroid species. Colour data in the text for the live specimens have been taken from these slides and from colour notes accompanying the other specimens.

## SYSTEMATIC ACCOUNT

### OPHIOMYXIDAE

#### **Ophiomyxa australis** Lütken

*Ophiomyxa australis* Lütken, 1869:99.—H. L. Clark, 1938:201, pl. 13, figs. 1,2; 1946: 170.—A. M. Clark & Rowe, 1971: 78, 92, pl. 13, figs. 3, 4.— Gibbs *et al.*, 1976: 114.

MATERIAL

Station 6-1 (J.8861).

A colour slide of the living specimen (disc diameter, 7.5 mm) is available: the disc and arms are finely speckled with pink and white and, in addition, prominent brown spots which remain in the dried material are present over the dorsal disc surface. The wide diversity of colouration exhibited by this species over its extensive distribution range has been described by H. L. Clark (1938) and, more recently, noted and illustrated by Coleman (1977:162).

### AMPHIURIDAE

#### **Amphioplus (Amphioplus) didymus** H. L. Clark

*Amphioplus didymus* H. L. Clark, 1938: 252, pl. 14, fig. 3, text-fig. 17; 1946: 206.

*Amphioplus (Amphioplus) didymus.* — A. M. Clark, 1970: 56. — A. M. Clark & Rowe, 1971: 78, 101, text-figs. 27g, 48d, e. — Gibbs *et al.*, 1976: 115, text-fig. 1a.

MATERIAL

Station 5-1 (J.8856); Station 6-1 (J.8885) (both lacking the dorsal disc surface).

This species has recently been recorded from the northern part of the Great Barrier Reef (Gibbs *et al.*, 1976) and the present material from the Swain Reefs represents a southward extension of its range.

Although the dorsal disc surface of both specimens is missing, several features readily identify this material as *A. (Amphioplus) didymus* in contrast to other closely related amphiurid species, particularly *A. (Amphioplus) stenaspis* H. L. Clark and *A. (Lymanella) bocki* Koehler (Gibbs *et al.*, 1976). These include: (1) the presence of four or five arm spines proximally, rapidly reducing in number to three; (2) the second from lowermost arm spine in each series beyond the arm base is abruptly squared off and provided with two glassy hooks, one directed towards the mouth and the other to the arm tip. It has been suggested that the bihamulate shape of the middle arm spines is the only reliable diagnostic criterion (Gibbs *et al.*, 1976).

A colour slide of the Station 5 specimen is available. The arms are bright yellow with very dark irregular markings along their dorsal surface and the arm spines are dark with pale tips. These colour notes accord with those reported for the holotype and paratype of the species with the exception that H. L. Clark (1938) described the dark markings as 'vermilion'.

### **Amphioplus (Amphichilus) ochroleuca** (Brock)
(Fig. 1,2)

*Amphiura ochroleuca* Brock, 1888: 484. — Koehler, 1904: 63, text-figs. 12, 13.

*Amphiura brocki* Döderlein, 1896: 286, pl. 15, figs. 6, 6a.

*Amphiodia mesopoma* H. L. Clark, 1915: 247, pl. 6, figs. 11, 13; 1918: 287, pl. 3, fig. 7.

*Amphiodia ochroleuca.* — H. L. Clark, 1915: 250. — Koehler, 1930: 105. — H. L. Clark, 1938: 247; 1946: 203.

*Amphioplus (Amphichilus) ochroleuca* A. M. Clark, 1970: 49, text-fig. 8t. — A. M. Clark & Rowe, 1971: 78, 100, text-fig. 48f, g.

MATERIAL

Station 6-1 (J.8884).

*Amphioplus (Amphichilus) ochroleuca* was first described from Amboina, East Indies (Brock, 1888). It has also been described under two synonyms: firstly, as *brocki*, from Thursday Island, Torres Strait (Döderlein, 1896) and later, as *mesopoma*, from Badu, Torres Strait (H. L. Clark, 1915). H. L. Clark (1915) also reported *mesopoma* from Spencer and St. Vincent Gulfs, South Australia, and Westernport, Victoria. The same author (H. L. Clark, 1938), having synonymized *brocki* and *mesopoma* with *ochroleuca*, reported the species from Darwin and Broome. Material in the West Australian Museum extends the species range along the west Australian coast as far south as Dunsborough. Along the east Australian coast, *ochroleuca* has now been recorded from the Swain Reefs and from off Port Hacking, NSW (Kingston, in preparation): the species thus has a practically circum-Australian distribution.

The genus *Amphichilus* was erected by Matsumoto (1917:175) for the Japanese species *trichoides* Matsumoto. A. M. Clark (1970), in her revision of the Amphiuridae, reduced *Amphichilus* to a subgenus of *Amphioplus* and, in addition, assigned the species *ochroleuca* to it. *Amphichilus* is very close in terms of its oral armament to *Unioplus* (another subgenus of *Amphioplus*), in that both taxa possess three oral papillae. Indeed in this regard there seems to be some confusion in the subgeneric allocation of *ochroleuca*. In A. M. Clark & Rowe's key (A. M. Clark & Rowe, 1971: 100), *Amphichilus* is distinguished from *Unioplus* using two criteria: (a) the relative size of the middle oral papilla; (b) the degree of contiguity of the radial shields. In *Amphichilus* the two distal oral papillae are similar in size but in *Unioplus* the middle oral papilla is described as the largest: the oral papilla referred to is the third oral papilla in that it attaches either wholly or partially to the edge of the adoral shield (the designation of jaw areas and explanation of amphiurid dental formulae is described in detail by A. M. Clark, 1970:5). In both *Amphichilus* and *Unioplus*, the second oral papilla is absent (A. M. Clark, 1970: 48, 49) but its place may appear to be taken by the first oral tentacle scale which may be placed at a

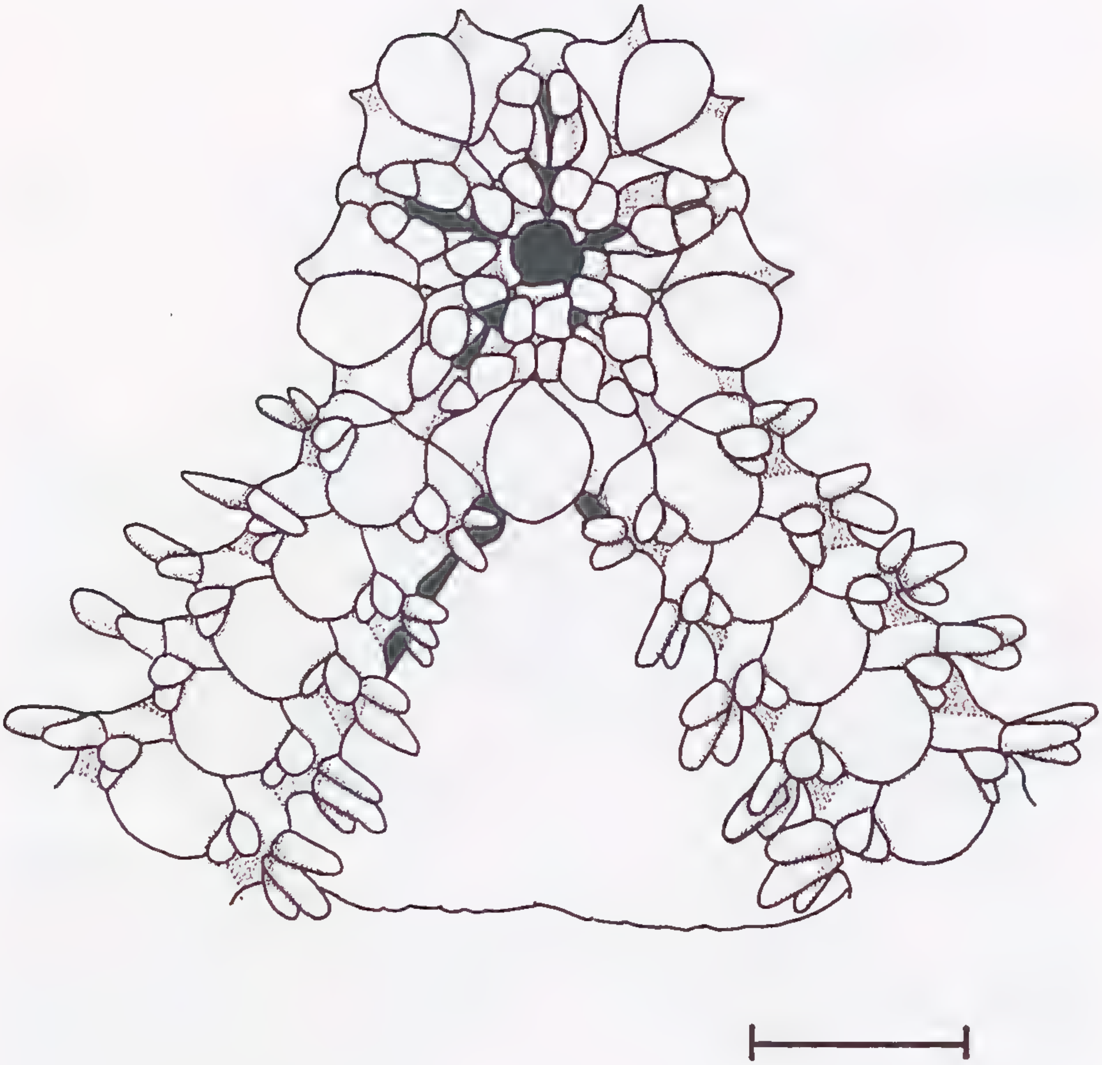


Fig. 1. *Amphioplus (Amphichilus) ochroleuca* (Brock). Ventral surface of the disc. Scale represents 1.0 mm.

relatively superficial level in the jaw such that it appears in line with the other oral papillae. In *ochroleuca,* both the position of the third oral papilla and the degree of prominence of the first oral tentacle scale is variable, even within Australian material. Thus, A. M. Clark (1970: 39, text-fig. 8t) describes the dental formula of *ochroleuca* as m,m,m,+t and illustrates prominent oral tentacle scales whilst in other Australian material examined, the dental formula is m, $\overline{N,N}$,m+t and the oral tentacle scales may not be as superfically placed in the jaw (Fig. 1) (where $\overline{N,N}$, indicates that the third oral papilla partially arises from both the side of the oral plate and the edge of the adoral shield and is enlarged). The relative enlargement of the third oral papilla pertains in only three of the thirteen species assigned to *Unioplus* (see the dental formulae given by A. M. Clark 1970: 37) yet it appears to be a consistent feature in *ochroleuca* formally assigned to *Amphichilus.* Thus Koehler (1904) who figured Brock's (1888) type of *ochroleuca* noted that 'la papille buccale moyenne (is) plus large que les autres'. It is also relevant that H. L. Clark (1925:247) described the middle oral papilla in *mesopoma* as the 'largest and lid-like'.

*Unioplus* and *Amphichilus* are further distinguished by the degree of contiguity of the radial shields: in *Unioplus,* the radial shields are separated or at least divergent whilst in *Amphichilus,* they are completely contiguous. Again, *ochroleuca* corresponds to *Unioplus* rather than *Amphichilus.* Koehler (1904) illustrated Brock's (1888) type specimen of *ochroleuca* as possessing radial shields separated by a narrow strip of somewhat enlarged scales, a condition that compares with material described as *mesopoma* by H. L. Clark (1915) and with other Australian material examined (Fig. 2). H. L. Clark (1938), in describing growth changes in this species, noted that at disc diameters of 4 mm or less the radial shields may be more or less in contact. Since the type specimen with a disc diameter of 9 mm is the largest specimen of *ochroleuca* presently recorded and the Australian material examined have disc diameters ranging from 4-6 mm, the degree of contiguity of the radial shields may be an ontogenetically related variable and not of strict taxonomic significance in this species. A. M. Clark (in A. M. Clark & Rowe, 1971:132, text-fig. 48f) in illustrating the dorsal disc surface of a 6 mm disc diameter specimen suggested that the partial contiguity of the radial shields may be an unusual feature.

The two subgenera are further distinguished by the degree of contiguity of the dorsal arm plates: in *Unioplus,* the arm plates are barely, if at all, in contact whilst in *Amphichilus* they are (A. M. Clark, 1970: 48). In this regard, *ochroleuca* can be assigned without doubt to *Amphichilus.*

Whilst the specific identity of the Swain Reefs specimen as *ochroleuca* is not in doubt, particularly when Koehler's (1904) notes and illustration of the type and H. L. Clark's (1915) description of *mesopoma* are considered, its subgeneric allocation appears to be rather tenuous. It is suggested that these subgenera may require re-evaluation perhaps using internal morphological features such as the dental and oral plates which do indicate generic relationships in other ophiuroid families, for example the Ophiotrichidae (Kingston, in preparation).

In the present material from the Swain Reefs, the disc (disc diameter, 5 mm) is marked with pale yellow and the arms are narrowly cross-banded with the same colour. Colour notes for the living specimen describe it as 'pinkish-cream with narrow red bands on the arms'. The considerable diversity in colouration shown by this species (discussed by H. L Clark, 1938: 248) may be the result of the fugacity of these pigments under different conditions of preservation.

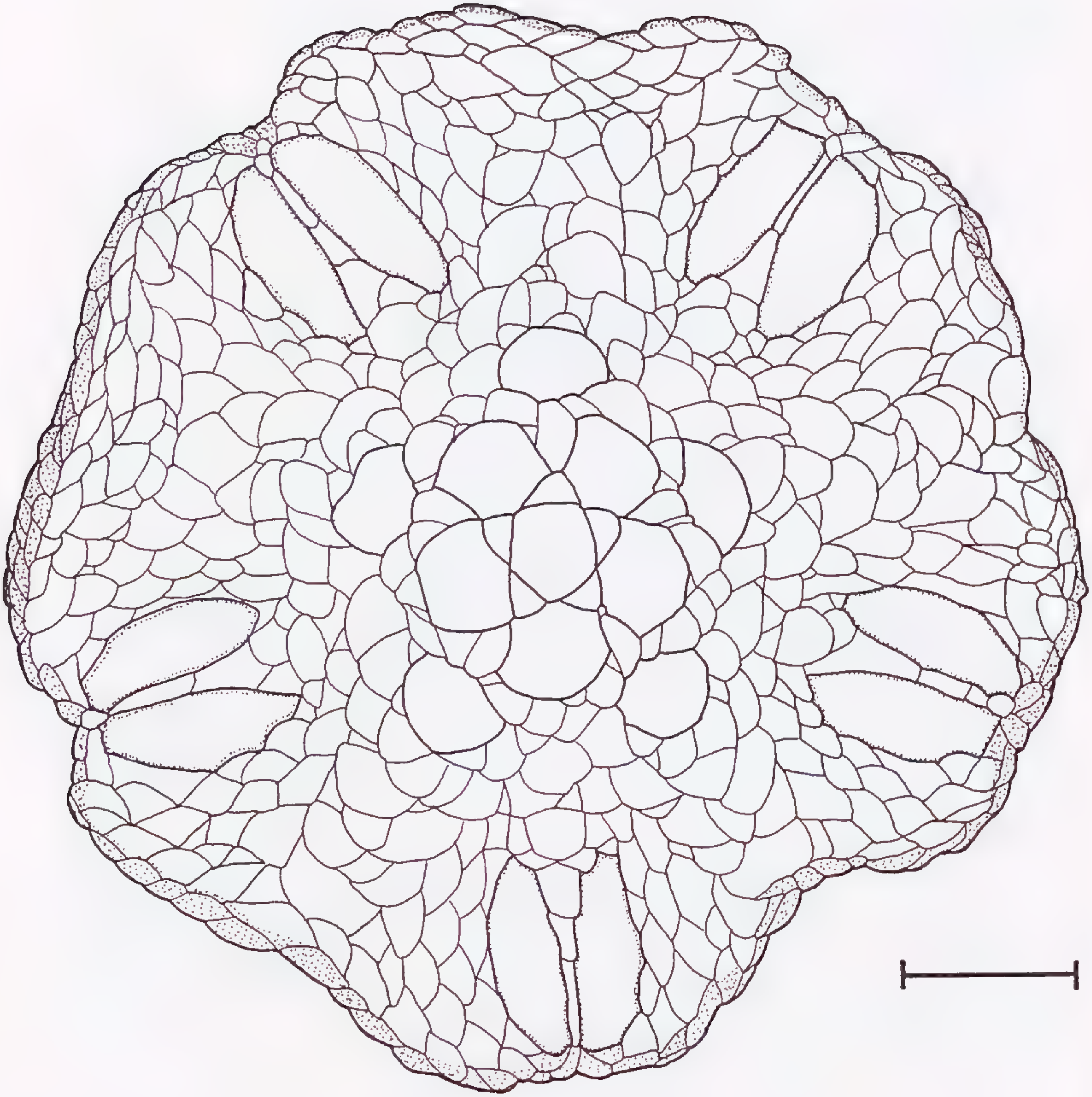


Fig. 2. *Amphioplus (Amphichilus) ochroleuca* (Brock). Dorsal surface of the disc. Scale represents 1.0 mm.

### **Amphiura (Amphiura) luetkeni** Duncan
(Fig. 3a,b)

*Amphiura lütkeni* Duncan, 1879: 464, pl. X, fig. 17.

*Amphiura (Amphiura) luetkeni*.—A. M. Clark & Rowe, 1971: 80, 97, pl. 13, figs. 6,7.

*Amphiura duncani* Lyman, 1882: 124, 132, 310. — Koehler, 1905: 33.— Matsumoto, 1917: 208.

MATERIAL

Station 7-1 (J.8887).

*Amphiura (Amphiura) luetkeni,* first described from Korean Seas, has subsequently been recorded from the East Indies, Philippine Islands, China and South Japan (A.M. Clark and Rowe, 1971). The Swain Reefs specimen, therefore, represents a new record for Australian waters.

The dorsal surface of the disc (disc diameter, 3.5 mm) is very finely scaled and no central rosette of primary plates is apparent; the fine scaling continues into the ventral interradii. The radial shields are banana-shaped, three times as long as broad and equal to half the disc radius. Distally, the radial shields of each pair are either not or only just contiguous: proximally, they are divergent and widely separated from each other. The two large, prominent infradental papillae are separated by a broad diastema from the second oral papillae on either side. The large pointed oral tentacle scale abuts onto the entire lateral margin of the oral plate. The oral plates are conspicuously sunken midway along their length, rising up to meet the adoral shields distally and for the insertion of the infradental papillae proximally (Fig. 3a). The ventral arm plates are longer than broad for the greater part of the arm length. There is one moderate sized tentacle scale. The dorsal arm plates are rounded pentagonal and the lateral and distal margins form a continuous fan shape; there is some overlap between succeeding plates (Fig. 3b). The lateral arm plates encroach upon the ventral and dorsal arm plates but do not meet either above or below. Proximally, there are six arm spines, which reduce in number to five and then four about halfway along the arm length. The spines are cylindrical with bluntly pointed rugose tips; the lowermost in each series is the longest and approaches one arm segment in length.

There are no colour notes for the living specimen and no colour remains in the dried material.

### **Dougaloplus echinatus** (Ljungman)

*Ophiophragmus echinatus* Ljungman, 1867: 316.

*Ophiocnida echinata.* — H. L. Clark, 1946: 203.

*Dougaloplus echinatus.*— A. M. Clark, 1970: 35, text-fig. 7h-k, ?l.— A. M. Clark & Rowe, 1971: 80, 100, text-fig. 26i.—Gibbs *et al.*, 1976: 123.

MATERIAL

Station 6-1 (J.8888).

The present record represents a further extension southward of the species' range in the Great Barrier Reef.

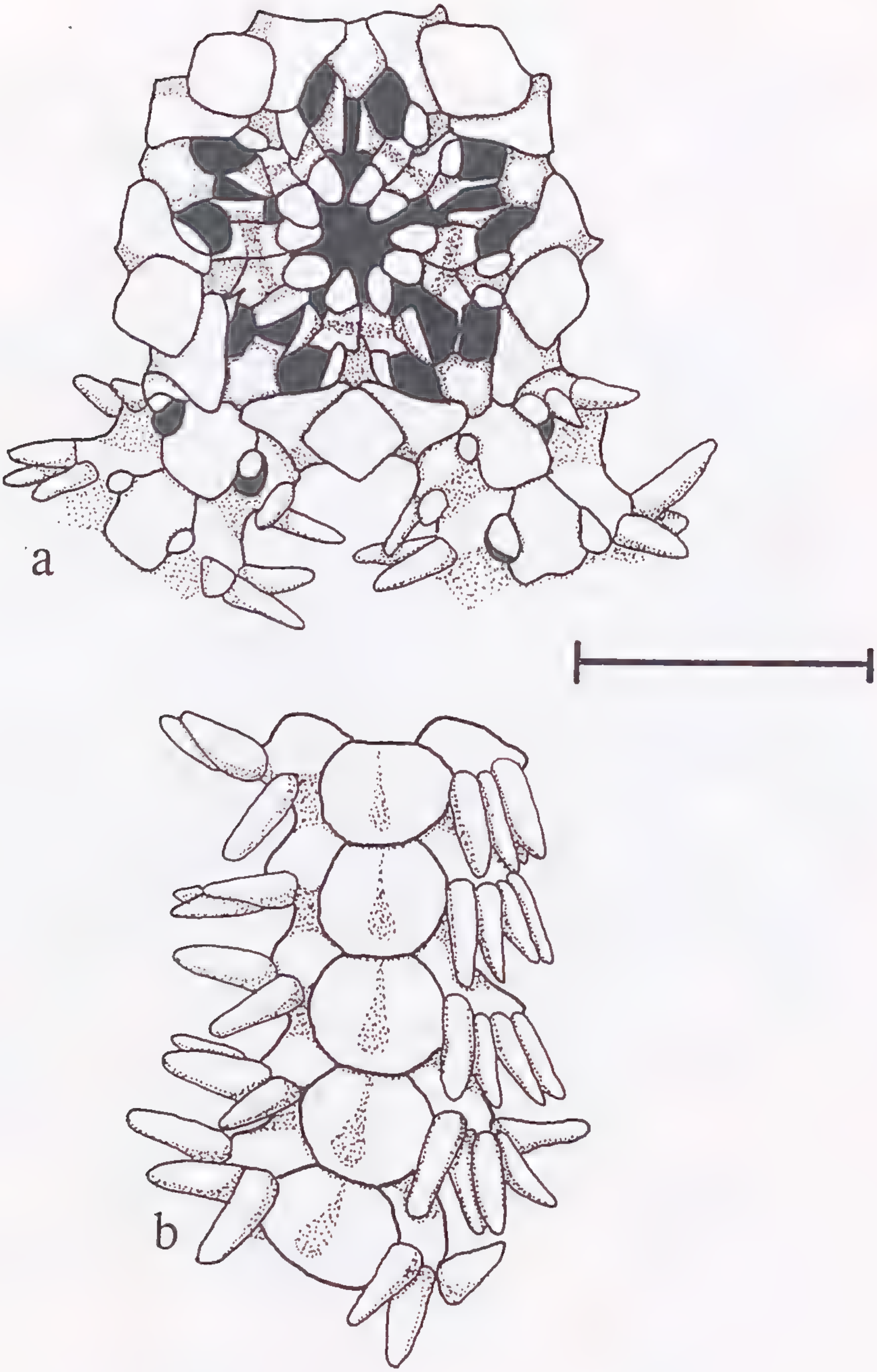


Fig. 3a *Amphiura (Amphiura) luetkeni* Duncan. Ventral surface of the disc. 3b. Dorsal surface of the arm, segments 5-9. Scale represents 1.0 mm.

## OPHIACTIDAE

### **Ophiactis savignyi** (Müller & Troschel)

*Ophiolepis savignyi* Müller & Troschel, 1842:95.

*Ophiactis savignyi.*— H. L. Clark, 1921: 108; 1938: 260; 1946: 210. — A. M. Clark & Rowe, 1971: 82, 103, pl. 14, fig. 4. — Gibbs *et al.*, 1976: 123.

MATERIAL

Station 4-1 (J.8883).

A live specimen of *Ophiactis savignyi* is illustrated in colour by Coleman (1977:165).

## OPHIOTRICHIDAE

### **Macrophiothrix longipeda** (Lamarck)

*Ophiura longipeda* Lamarck, 1816: 544.

*Macrophiothrix longipeda.* — H L. Clark, 1921: 110, pl. 15, fig. 5, pl. 33, fig. 1; 1938: 288; 1946: 221. — A. M. Clark, 1967: 648, pl. 11, fig. 1, text-fig. 1m. — A. M. Clark, 1968: 300, figs. 3 m-o, 4 p-r, 5 p-r, 7l, m. — A. M. Clark & Rowe. 1971:82, 114, pl. 16, fig. 4, text-figs. 35 f, 37 l.

MATERIAL

Station 1-1 (J.8903); Station 6-2 (J.8904); off Gillett Cay-1 (J.7585).

Colour slides are available of the dorsal and ventral aspect of one specimen (J.8904). The radial shields are marked with blue and yellow blotches and black spots; the remainder of the disc is dirty brown. The arms are cross-banded with brown and dark blue upon which black spots, each surrounded by a yellow rim, are irregularly distributed. Ventrally, the disc is brown and the arms similarly cross-banded with brown and deep blue. The extended tube-feet are bright blue. In the dried specimen, the brown has changed to blue and the yellow rims around the black spots have entirely disappeared.

### **Ophiothela danae** Verrill

*Ophiothela danae* Verrill, 1869: 391.— A. M. Clark & Rowe, 1971: 84, 116, pl. 14, fig. 5. — A. M. Clark, 1976: 112. — Gibbs *et al.*, 1976: 125.

*Ophiothela hadra* H. L. Clark, 1915: 284, pl. 14, fig. 2; 1921: 117, pl. 13, fig. 5; 1938: 319.

MATERIAL

Station 6-1 (J. 8891).

Under its synonym *Ophiothela hadra, Ophiothela danae* (A.M. Clark, 1976) has been recorded from the east Australian coast as far south as Ballina, New South Wales (H. L. Clark, 1921, 1938; Endean, 1953, 1957). The Swain Reefs specimen falls within this range.

From a colour slide of the living specimen, the dorsal disc is red centrally and marbled with white, yellow and black towards its perimeter. The dorsal surface of the arms is cross-banded with yellow, white and black. In the dried specimen, the red colouration is reduced to pale pink; the yellow has entirely disappeared; and the black changed to blue. The considerable alterations in disc and arm pigmentation brought about by preservation in alcohol may explain the frequently observed mismatch in colouration between *Ophiothela danae* and the gorgonians upon which this brittlestar is commonly epizoic (for example Gibbs *et al.*, 1976). H. L. Clark (1921) also noted that a marked change in colouration is effected by preservation, the green and yellow tints of the living material becoming pale rose and grey.

### **Ophiothrix ciliaris** (Lamarck)

*Ophiura ciliaris* Lamarck, 1816:545.

*Ophiothrix stelligera* Lyman, 1874:237, pl. 3, figs. 15-20. — H. L. Clark, 1921:114, pl. 16, fig. 8; 1938: 273; 1946: 216.

*Ophiothrix ciliaris*. — A. M. Clark, 1967:646. — A. M. Clark & Rowe, 1971: 84, 109, text-fig. 35a.

MATERIAL

Station 1-1 (J.8892); Station 4-1 (J.8893); Station 6-3 (J.8894-8896).

Under its synonym, *Ophiothrix stelligera, Ophiothrix ciliaris* has been recorded for the Great Barrier Reef from the Murray Islands (H. L. Clark, 1946). The Swain Reefs material represents a considerable southward extension of its range in the Great Barrier Reef.

A colour slide is available of one of the living Station 6 specimens. The disc is pale cream with dark brown spots. The dorsal surface of the arms is marked with two longitudinal dark brown stripes either side of the midline which is yellow where it overlies faint cross-bands produced by an increased red colouration. In the dried specimen, nearly all the colouration has disappeared and only the dorsal disc spots and brown arm stripes remain; even these are rather faded. H. L. Clark (1938) similarly noted that the red and pink colouration of living material disappears on preservation, leaving only brown or dull purple shades.

### **Ophiothrix (Acanthophiothrix) proteus** Koehler

*Ophiothrix comata*.— Koehler, 1898: 105, pl. 2, figs. 11-14 (non *Ophiothrix comata* Müller & Troschel).

*Ophiothrix proteus* Koehler, 1905: 100.— H. L. Clark, 1915: 277.

*Ophiothrix (Acanthophiothrix) proteus*.— A. M. Clark, 1967: 648.—A. M. Clark & Rowe, 1971: 84, 111, pl. 15, fig. 5.— Gibbs *et al.*, 1976: 126.

MATERIAL

Station 6-2 (J.8898).

*O. (Acanthophiothrix) proteus* has recently been recorded from the northern part of the Great Barrier Reef (Gibbs *et al.*, 1976) and the present material represents a southward extension of its range.

From a colour slide of one of the living specimens, the dorsal surface of the arm is boldly marked with two longitudinal orange stripes separated by a broad white stripe running along the midline. In addition, the arms are broadly cross-banded due to the intensification of the red-orange ground colour of the arms. A similar increase in pigmentation is present in the adjoining arm spines of these darker arm segments. The disc is pale cream marked with single orange stripes that continue inwards from the double orange stripes of the arms between each of the radial shields of a pair. In addition, each radial shield is marked with rows of small dark brown spots that regularly radiate out from its adradial distal corner. In the dried specimens, much of this colouration has disappeared leaving only two dark purple longitudinal stripes running either side of the midline of the dorsal arm surface.

### **Ophiothrix (Keystonea) martensi australis** H. L. Clark

*Ophiothrix martensi australis* H. L. Clark, 1921: 111, pl. 15, fig. 4.

*Ophiotrichoides martensi australis.*—H. L. Clark, 1938:305; 1946: 231.

*Ophiothrix (Keystonea) martensi australis*.—A. M. Clark & Rowe, 1971: 86, 107, text-fig. 34d.

MATERIAL

Station 6-1 (J.8899).

Colour slides of both the ventral and dorsal aspect of the living specimen are available. The dorsal surface of the disc is pale blue with dark blue lines radiating out from its centre that continue along the dorsal midline of the arms with the zigzag pattern characteristic of this subspecies (H. L. Clark, 1938). Both on the disc and more prominently on the arms, these longitudinal blue markings are bordered with orange. At its perimeter and in the ventral interradii, the disc is variegated with blue and orange. A broad blue stripe runs along the entire ventral arm surface. In the dried specimen, the orange pigmentation has entirely disappeared and is replaced with pale blue.

### **Ophiothrix (Keystonea) nereidina** (Lamarck)

*Ophiura nereidina* Lamarck, 1816: 544.

*Ophiothrix nereidina.*— H. L. Clark, 1921: 112, pl. 15, figs. 2, 8, 9.

*Ophiotrichoides nereidina.*— H. L. Clark, 1938:306; 1946: 232.

*Ophiothrix (Keystonea) nereidina.*—A. M. Clark, 1967: 648, fig. 1l,—A. M. Clark & Rowe, 1971:86, 107, text-fig. 34b.

MATERIAL

Station 5-1 (J.8900); Station 6-1 (J.8901).

### **Ophiothrix (Placophiothrix) striolata** Grube

*Ophiothrix striolata* Grube, 1868: 45.—H. L. Clark, 1921: 114, pl. 15, fig. 1.

*Placophiothrix striolata.*— H. L. Clark, 1938: 314; 1946: 225.

*Ophiothrix (Placophiothrix) striolata.*—A. M. Clark: 1967: 648.—A. M. Clark & Rowe, 1971: 86, 113.

MATERIAL

Station 4-2 (J.8906, J.8907); Station 6-4 (J.8908-J.8911).

Endean (1957) classified *O. (Placophiothrix) striolata* as a 'mainland' species with a distribution south from Torres Strait to Lindeman Island. The Swain Reefs record suggests that this species should also be considered a 'reef' species. In addition, it represents a southward extension of its range in the Great Barrier Reef.

A colour slide is available of one specimen (J.8910). The dorsal surface of the arms is regularly cross-banded with brown and white speckled segments alternating with yellow segments marked with bold blue blotches either side of the midline. The prominent radial shields are marked with yellow and brown speckling. Distally, each shield has a central blue blotch; proximally, a similar blue marking extends across the shields of each pair. In the dried material the yellow and brown colouration has entirely disappeared, leaving the disc and arms white with pale blue markings. H. L. Clark (1938) has commented on the considerable colour changes effected by preservation in this species.

## OPHIOCOMIDAE

### **Ophiocoma dentata** Müller & Troschel

*Ophiocoma dentata* Müller & Troschel, 1842: 99.—Devaney, 1970: 13.— A. M. Clark & Rowe, 1971: 86, pl. 18, figs. 2, 3.— Gibbs *et al.*, 1976: 128.

*Ophiocoma brevipes* var. *variegata* H. L. Clark, 1921: 130.

*Ophiocoma insularia* var. *variegata* H. L. Clark, 1938: 330; 1946: 246.

MATERIAL

Station 1-4 (J.7376, J.8865-J.8866); Station 8-2 (J.8864).

### **Ophiocoma erinaceus** Müller and Troschel

*Ophiocoma erinaceus* Müller and Troschel, 1842: 98.—H. L. Clark, 1915: 291, pl. 15, figs. 5,6; 1921: 127; 1938: 329; 1946: 244.—A. M. Clark & Rowe, 1971: 86, 119, pl. 17, figs. 5,6.—Gibbs *et al.*, 1976: 128.

MATERIAL

Station 1-6 (J.8867, J.8869-J.8870); Station 8-4 (J.8868).

### **Ophiocoma scolopendrina** (Lamarck)

*Ophiura scolopendrina* Lamarck, 1816: 544.

*Ophiocoma scolopendrina*.—H. L. Clark, 1915: 293, pl. 14, figs. 10,11; 1921: 125, pl. 13, fig. 9; 1946: 243.—A. M. Clark & Rowe, 1971: 86, 128, pl. 14, figs. 3,4.

MATERIAL

Station 1-1 (J.7375); off Gillett Cay-1 (J.7140).

### **Ophiomastix caryophyllata** Lütken

*Ophiomastix caryophyllata* Lütken, 1869: 99.—H. L. Clark, 1921: 137, p. 14, fig. 4., pl. 36, fig. 10; 1946: 249.—A. M Clark & Rowe, 1971: 86, 120.

MATERIAL

Station 1-1 (J.8872).

*Ophiomastix caryophyllata* has been recorded from the Murray Islands (H. L. Clark, 1946), Low Isles (Endean, 1961), and Heron Island (Endean, 1965). The Swain Reefs record represents a further southward extension of the species' range.

In the dried specimen, the disc is creamy yellow with dark brown spots, both dorsally and ventrally. The sharply pointed disc spines are a uniform pale cream. The entire distal half of each dorsal and ventral arm plate is pale cream and strongly contrasts with the dark brown colouration of the proximal half of the arm segment. The four arm spines in each series are distinctly banded with dark brown on cream. The uppermost spines are conspicuously enlarged and clavate and are further distinguished by their more uniform dark colouration.

### **Ophiomastix luetkeni** Pfeffer

*Ophiomastix luetkeni* Pfeffer, 1910: 83.—H. L. Clark, 1915: 296, pl. 16, figs. 3,4; 1921: 136.—A. M. Clark & Rowe, 1971:86, 120, pl. 19, fig. 1.

MATERIAL

Station 1-2 (J.8871); 1974-1 (J.8689).

*Ophiomastix luetkeni* has previously been recorded from the East Indies, Philipine Islands, China and South Japan (A. M. Clark & Rowe, 1971). The present material, therefore, represents an extension of the species' range to Australian waters.

The Swain Reefs specimens were compared with specimens of *O. luetkeni* from the Solomon Islands (loaned from the British Museum (Natural History) by courtesy of Miss A. M. Clark). In all the specimens, the majority of the uppermost arm spines are greatly elongate and enlarged compared to the other arm spines of each series but only very rarely are these spines conspicuously thickened and clavate. The arm spines are banded but frequently this is rather indistinct. The colour throughout the dried specimens is very dark brown with narrow light brown to pale cream markings along the distal margins of the dorsal and ventral arm plates and between succeeding side arm plates. The sharply pointed disc spines are either a uniform pale or dark colour.

*O. luetkeni* is distinguished from *O. janualis* Lyman, which also lacks clavate upper arm spines, by the banding of its arm spines (A. M. Clark and Rowe, 1971). In both *O. caryophyllata* Lütken and *O. corallicola* H. L. Clark, which have also been reported from Australian waters, the upper arm spines are regularly and conspicuously clavate (A. M. Clark & Rowe, 1971).

### **Ophiopsila gilletti,** sp.n.

(Fig. 4a, b, c)

TYPE MATERIAL

Station 4-1. Gillett Cay adjacent to Station 3, dredged, at 36.5 m depth. Holotype T.A.M. reg. no. J.8873.

## DIAGNOSIS

A species of *Ophiopsila* with ventral interbrachia transparent and sparsely scaled; both tentacle scales erect, the outer, fine and spiniform, the inner, spatulate and with a 'mid-rib'; numerous clustered dental papillae and two lateral, thin, blunt-tipped oral papillae. The holotype is dried from alcohol.

## DESCRIPTION

Disc diameter c. 5 mm, distorted dorsally. Arm length c. 20 mm (d.d: a.l. = 1:4). Dorsally, the disc is densely covered with fine, imbricating scales. Ventrally, a small triangular area of sparsely scaled, transparent skin in each interbrachium delineated by the distal margin of the oral shields and the large opaque scales bordering the proximal quarter of the genital clefts (Fig. 4a). The radial shields are narrow (length 0.1 mm, breadth 0.01 mm), tapering proximally where they are encroached upon by the disc scales. The shields of each pair are separated by one or two rows of enlarged disc scales. The dorsal arm plates are longer than broad and contiguous throughout the length of the arm. Proximally, each lateral arm plate bears ten arm spines, reducing to eight or nine at the arm tip. All the arm spines are broadly flattened, blunt-tipped and minutely serrated over their entire surface. In each series, the lowermost spine is the longest, approaching one and a half times the segment length. The spatulate form of the arm spines is most developed in the second and third uppermost spines of each series. The five or six middle arm spines of each series are approximately identical in morphology and dimensions (Fig. 4b). All the arm spines are erect and are not adpressed to the arm surface. The ventral arm

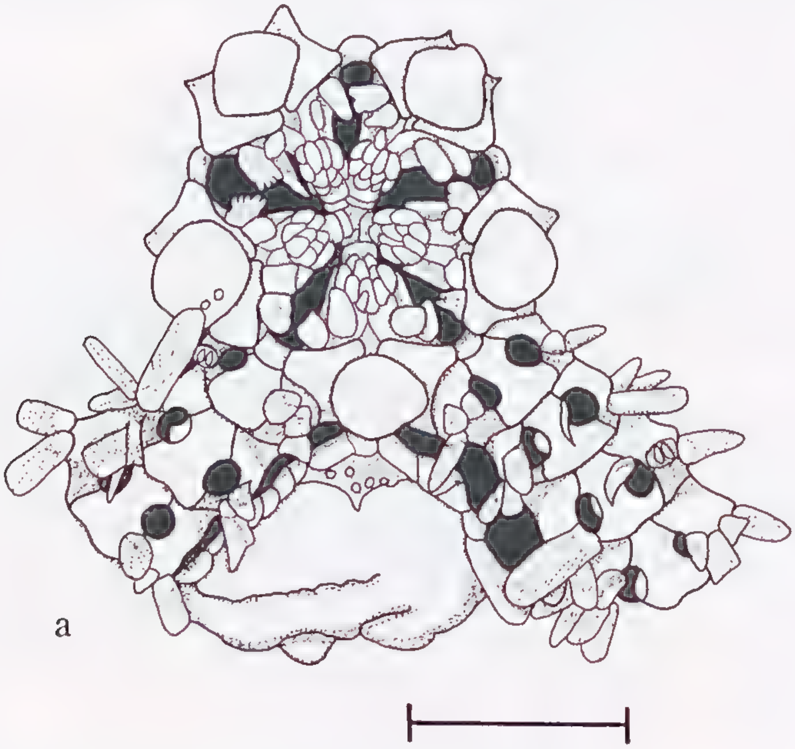
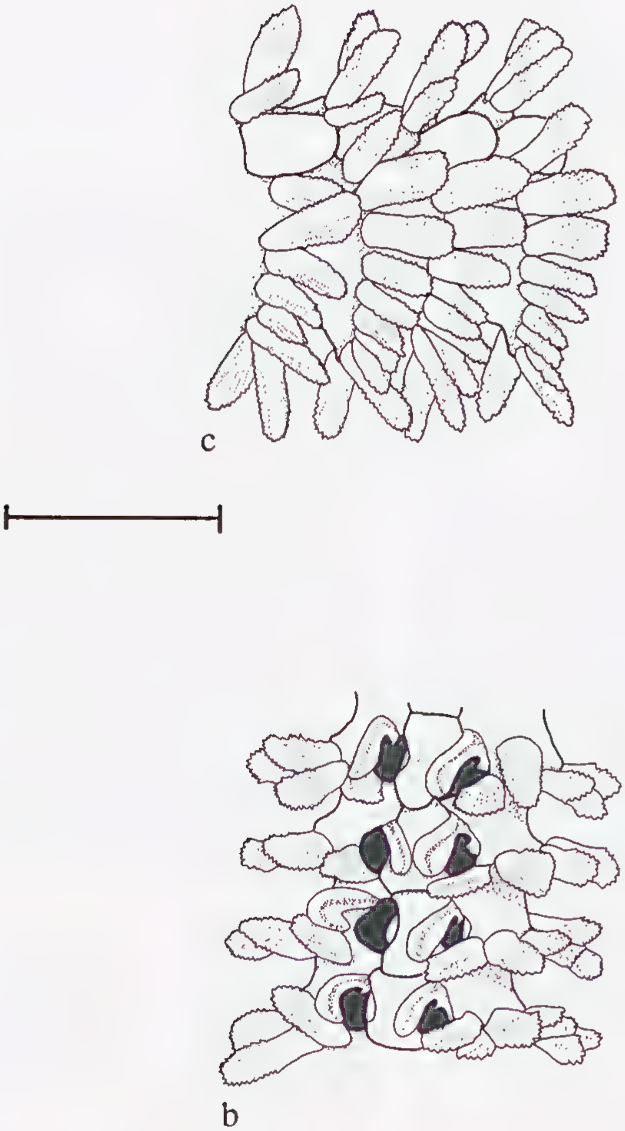


Fig. 4a. *Ophiopsila gilletti sp.n.* Ventral surface of the disc.



4b. Ventral surface of the arm, midway down its length.
4c. Arm in profile, segments, 5-7. Scale represents 1.0 mm.

plates are longer than wide, their distal margins becoming somewhat concave towards the arm tip. The tentacle pores are large. Two tentacle scales are present: the outer is thin and spiniform; the inner is thin, spatulate and bears a distinct 'midrib' on its ventral surface (Fig. 4c). The inner tentacle scales are usually erect but occasionally lie flat on the ventral arm surface. The inner and outer tentacle scales on each side appear to be joined basally by a fine membrane: this membrane is not derived from the tube-foot and may be a preservation artefact. A small, semilunar scale may be present bordering the central inner margin of the tentacle pore. The oral shield is distinctly broader than long. The proximal margin is gently rounded; the distal margin is slightly prolonged to form a broad lobe. The adoral shields approach each other closely interradially above the oral shields but are not contiguous. The oral plates bear eight or nine clustered, small, slender, dental papillae. Each adoral shield bears two lateral, thin, broad, blunt-tipped oral papillae. In several jaw sectors, the lateral papillae are split at the tip. The colour of the dried holotype is pale fawn with sinuous orange-brown markings; the radial shields are pale fawn. The arms are cross-banded at two to three segment intervals with orange-brown and chocolate brown. The arm spines are white with a faint orange cross-band about a third of the way up from the spine base. Ventrally, the arms and mouth region are white. Towards the arm tip, the cross-banding of the dorsal arm surface appears ventrally.

There are no colour notes for the live specimen.

The highly distinctive ophiocomid genus *Ophiopsila* Forbes has not been recorded previously from Australian waters although its members are widespread through tropical and temperate regions (H. L. Clark, 1915, 1918; Koehler, 1930; Baker, 1974). *O. novaezealandicae* from New Zealand (Baker, 1974), and two South African species, *O. seminuda* (A. M. Clark, 1952) and *O. bispinosa* (A. M. Clark, 1974), have recently been added to the extensive species list. As Baker (1974) has noted, the genus may well require revision since many of its species are known from only one or two specimens. In addition, there is evidence that spine number, frequently used to differentiate species in this genus (e.g. H. L. Clark, 1918), may vary with disc diameter. One hesitates to add a further species to the considerable array of species already described but the present Swain Reefs specimen differs in several aspects from these known taxa. The discovery of additional Australian material of this genus may further elucidate the status of the Swain Reefs specimen.

Thus, *O. gilletti* differs from *O. novazealandicae* Baker in that: (1) the radial shields taper proximally rather than being rectangular and are not surrounded by distinctly different sized disc scales; (2) the dorsal arm plates are longer than broad throughout the entire arm length and are not obscured or separated by skin; (3) there are two lateral oral papillae compared to three to five in *O. novazealandicae*.

The new species compares closely with the South African *O. seminuda* A. M. Clark in that the ventral interbrachia are naked and the number and morphology of the arm spines are similar. However, the dorsal arm plates in *O. seminuda* are broader than long, the opposite condition to that found in *O. gilletti*.

With its numerous clustered dental papillae and two oral papillae, *O. gilletti* is close to two Indo-Pacific species: *O. polyacantha* H. L. Clark (1918) from the Dutch East Indies; and *O. pantherina* Koehler (1898) from the Mergui Archipelago. It differs from the former in the spatulate rather than slender morphology of the arm spines and from the latter in that the ventral interbrachia are sparsely rather than completely scaled and in the higher number of arm spines.

The species is named, as is its type locality, Gillett Cay, for Keith Gillett, leader of the Swain Reefs Expedition.

## OPHIONEREIDAE

### **Ophionereis intermedia** A. M. Clark

*Ophionereis intermedia* A. M. Clark, 1953: 90, text-fig. 12.

MATERIAL

Station 4-1 (J.8863).

*Ophionereis intermedia* was described by A. M. Clark (1953) from a single specimen collected at 80 m in the Tsuguru Strait, North Japan. The present record, therefore, represents a considerable extension in the species range to Australian waters.

Although the disc of the Swain Reefs specimen (disc diameter 2 mm; minimum arm length 12 mm) is quite badly distorted and much of its dorsal aspect missing, small, needle-like genital papillae are clearly visible edging the genital slits in two of the ventral interradii. Morphologically, *O. intermedia* closely resembles *O. dubia* (Müller & Troschel) which has been reported from the north-west Australian coast (H. L. Clark, 1946) and the Great Barrier Reef (Gibbs *et al*., 1976). Indeed, from the dorsal aspect, the two species are indistinguishable (A. M. Clark, 1953). Both possess extremely fine disc scaling and accessory scales that are inserted at the distal margins of the supplementary arm plates. The two species are principally distinguished by the presence of needle-like genital papillae in *O. intermedia;* genital papillae are entirely lacking in *O. dubia*. In addition to this feature, *O. intermedia* may be distinguished from *O. dubia* by the form of its ventral arm plates (A. M. Clark, 1953; pers comm.) and by the positioning of the tentacle scale relative to the ventral arm plate. Further records of *O. intermedia* in Australian waters have been identified in the collections of The Australian Museum; this material will be described and extensively discussed elsewhere (Kingston, in preparation).

### **Ophionereis lineata** H. L. Clark

*Ophionereis lineata* H. L. Clark, 1946: 238.—A. M. Clark & Rowe, 1971: 88, 122, text-fig. 56a-e.

MATERIAL

Station 6-1 (J.8874).

A. M. Clark (in A. M. Clark & Rowe, 1971) suggested that *Ophionereis lineata* was indistinguishable from *Ophionereis fusca* Brock but that this synonymy could only be confirmed after further examination of *O. fusca* from its type locality, Amboina. Because of this, the Swain Reefs specimen is presently referred to *O. lineata* although its extremely close resemblance to *O. fusca* is fully acknowledged by the present author. If *O. lineata* should prove to be synonymous with *O. fusca*, then H. L. Clark's (1946) record for Lindeman Island will provide an extension of range for *O. fusca* from the East Indies, and Philipine and South Pacific Islands to Australian waters. This would be confirmed by the Swain Reefs record which, in turn, would represent a further southward extension into the Great Barrier Reef.

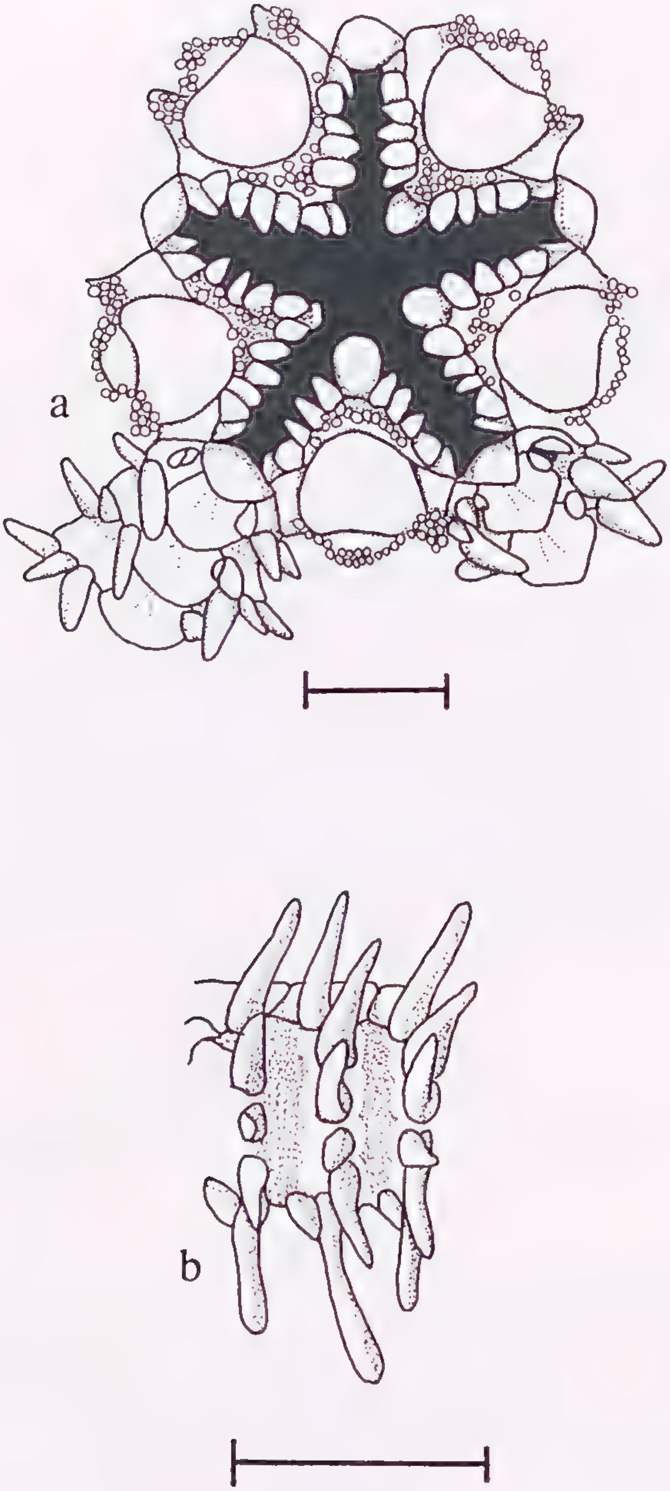


Fig. 5a. *Ophiarachnella macracantha* H. L. Clark. Ventral surface of the disc. 5b. Arm in profile, midway down its length. Scale represents 1.0 mm.

MATERIAL

Station 4-1 (J.8879).

*Ophioconis cincta* has previously been reported from Broome and Darwin (H. L. Clark, 1946). The Swain Reefs record represents an extension of its range to the Great Barrier Reef.

Although the disc is rather badly distorted in the present specimen (disc diameter 3.5 mm approximately), marginal disc spinelets are clearly visible. In addition, a very few spinelets are scattered over the dorsal surface of the disc. The highly variable occurrence and distribution of disc spinelets in this species noted by H. L. Clark (1938) has been discussed by A. M. Clark (1965). In the dried specimen, the disc and arms are white with grey-brown widely spaced, narrow cross-bands on the arms. There are no colour notes for the living specimen.

### **Ophiodyscrita pacifica** (Murakami)

(Fig. 6a, b)

*Ophiocryptus pacificus* Murakami, 1943:188, text-fig. 10.

*Ophiodyscrita pacifica.* — A. M. Clark & Rowe, 1971:88, 128.

MATERIAL

Station 5-1 (J.8880)

*Ophiodyscrita pacifica* was first reported from Palao by Murakami (1943). The Swain Reefs specimen, therefore, represents a new record of the species for Australian waters.

In the present specimen, disc diameter is 5 mm; the arms are all broken off within 10 mm of the disc. Although the disc is badly damaged dorsally its granulation is pronounced, extending ventrally to cover the entire mouth apparatus and continuing along the arms. The dorsal arm plates are triangular and are heavily encroached upon by the granulated lateral arm plates which meet both above and below the arm. The five conical arm spines of each series are very small and only approach one third of the length of the arm segment. For the greater length of the arm there is only one tentacle scale (Fig. 6a, b).

*O. pacifica* primarily differs from the closely related Australian species, *O. acosmeta* H. L. Clark, reported from Broome (H. L. Clark, 1938:356) in that at similar disc diameters, *O. acosmeta* has eight arm spines compared to the five or six in *O. pacifica*. The holotype of *O. acosmeta* (figured in A.M. Clark & Rowe, 1971: 100, text-fig. 54d-f) was available for examination (on loan from the Museum of Comparative Zoology, Harvard). In addition to differences in arm spine number, the two species also differ in the form of the dorsal and ventral arm plates. In *O. pacifica*, the dorsal arm plates are fully exposed and are triangular in shape; in *O. acosmeta*, the plates are exposed only to the extent of a restricted elliptical area. The ventral arm plates in *O. pacifica* are elongate pentagonal in shape whereas in *O. acosmeta*, they approach an almost circular form (Fig. 6a, b).

No trace of colour remains in the dried specimen but a colour slide of the living specimen shows the dorsal surface of the disc to be brick red and the arms broadly cross-banded with pink and white. Murakami (1943) describes the disc of *O. pacifica* as "dirty grey with the arms cross-banded with light grey and light brownish olive". It is not known whether the colours of the living specimen would fade to those described for dried material: Certainly in the Swain Reefs specimen, the living colours are entirely fugacious.

The Swain Reefs specimen (disc diameter 7 mm; arm length (broken) 30 mm) closely compares with H. L. Clark's (1946) description and A. M. Clark & Rowe's (1971) figure of the holotype from Lindeman Island with one exception: the genital papillae, although extending along the entire length of the genital slit, do not continue around to the dorsal surface of the arm. It is highly probable that this feature may be due to the comparatively small disc diameter of the Swain Reefs specimen. In both the holotype of *O. lineata* and two specimens of *O. fusca* (loaned from the British Museum (Natural History) by courtesy of Miss A. M. Clark) in which the disc diameter ranges from 8.5-10 mm, a palisade of genital papillae is clearly visible above the dorsal arm surface as it emerges from the disc.

The two species differ principally in their colouration. *O. fusca* has a spotted disc and dorsal arm plates, togther with banded arm spines. In the dried specimen of *O. lineata,* the disc is similarly spotted and marked with brown; the arms are broadly cross-banded and display a longitudinal stripe along the midline; the arm spines are not banded (H. L. Clark, 1946).

## OPHIODERMATIDAE

### **Ophiarachna megacantha** H. L. Clark

*Ophiarachna megacantha* H. L. Clark, 1938: 341, text-figs. 28-30; 1946: 254.

MATERIAL

Station 6-3 (J.8875-J.8876).

*Ophiarachna megacantha* has previously been recorded from off Double Island Point and Lindeman Island in the Great Barrier Reef (H. L. Clark, 1938; 1946). The Swain Reefs specimens fall midway between these presently recorded furthest south and north limits of the species range. Endean (1957) classed *O. megacantha* as a 'mainland' species; the present record suggests that it also be classified as a 'reef' species.

The three Swain Reefs specimens compare closely with the holotype and a paratype of the species placed in the collections of The Australian Museum.

There are no colour data for the living specimens.

### **Ophiarachnella infernalis** (Müller & Troschel)

*Ophiarachna infernalis* Müller & Troschel, 1842: 105.

*Ophiarachnella infernalis*.—H. L. Clark, 1909: 124; 1921: 142; 1938: 347; 1946: 262.—A. M Clark & Rowe, 1971: 88, 125, text-fig. 43a.—Gibbs *et al.,* 1976: 129.

MATERIAL

Station 6-1 (J.8877).

The present record represents a further southward extension of the species range from that reported by H. L. Clark (1946) and Gibbs *et al.* (1976).

Colour notes with the living specimen describe it as 'medium and dark brown'.

### **Ophiarachnella macracantha** H. L. Clark
(Fig. 5a,b)

*Ophiarachnella macracantha* H. L. Clark, 1909: 126.—A. M. Clark & Rowe, 1971: 88, 126.

MATERIAL

1974-1 (J.8688).

*Ophiarachnella macracantha* has previously been recorded from the Caroline Islands in the South Pacific (H. L. Clark, 1909) and the present record represents a new extension of range to Australian waters.

The Swain Reefs specimens compares closely with two paratypes of *Ophiarachnella macracantha* loaned by the Museum of Comparative Zoology, Harvard (this previously unfigured species will be illustrated elsewhere (Kingston in preparation). In the dried specimen (disc diameter, 13 mm; arm length, 58 mm,) the disc is pale grey above with exposed, almost circular, dark grey radial shields. In addition, a star-shaped dark grey marking with the points of the star aligned between the members of each pair of radial shields is present on the disc surface. The arms are grey dorsally and broadly crossbanded with darker grey. The fine but dense granulation of the dorsal surface continues into the ventral interradii up to the supplementary oral shields which are exposed. There is a maximum of seven arm spines proximally but for the greater part of the arm length, six arm spines are present in each series.

The lowermost spine is the longest and equal to one and half times the arm segment length (Fig. 5a, b).

### **Ophiochasma stellatum** (Ljungman)

*Ophiarachna stellata* Ljungman, 1867: 305.

*Ophiochasma stellata*.— H. L. Clark, 1909: 121.

*Ophiochasma stellatum*.—H. L. Clark, 1921: 141; 1938: 345; 1946: 259.— A. M. Clark & Rowe, 1971: 88, 124, pl. 20, fig. 1.—Gibbs *et al.*, 1976: 129.

MATERIAL

Station 6-1 (J.8878).

Endean (1957) classed *Ophiochasma stellatum* as a 'mainland' species; the present material from Swain Reefs, however, suggests its inclusion as a 'reef' species. In addition, this record represents an extension of range southward from the species' previously recorded distribution (Endean, 1965; Gibbs *et al.*, 1976).

### **Ophioconis cincta** Brock

*Ophioconum cinctum* Brock, 1888: 480.
*Ophiurodon cinctum* Matsumoto, 1917: 315. — H. L. Clark, 1938:339.
*Ophioconis cincta*. — H. L. Clark, 1946:255. — A.M. Clark & Rowe, 1971:88,127, text-fig. 44f.

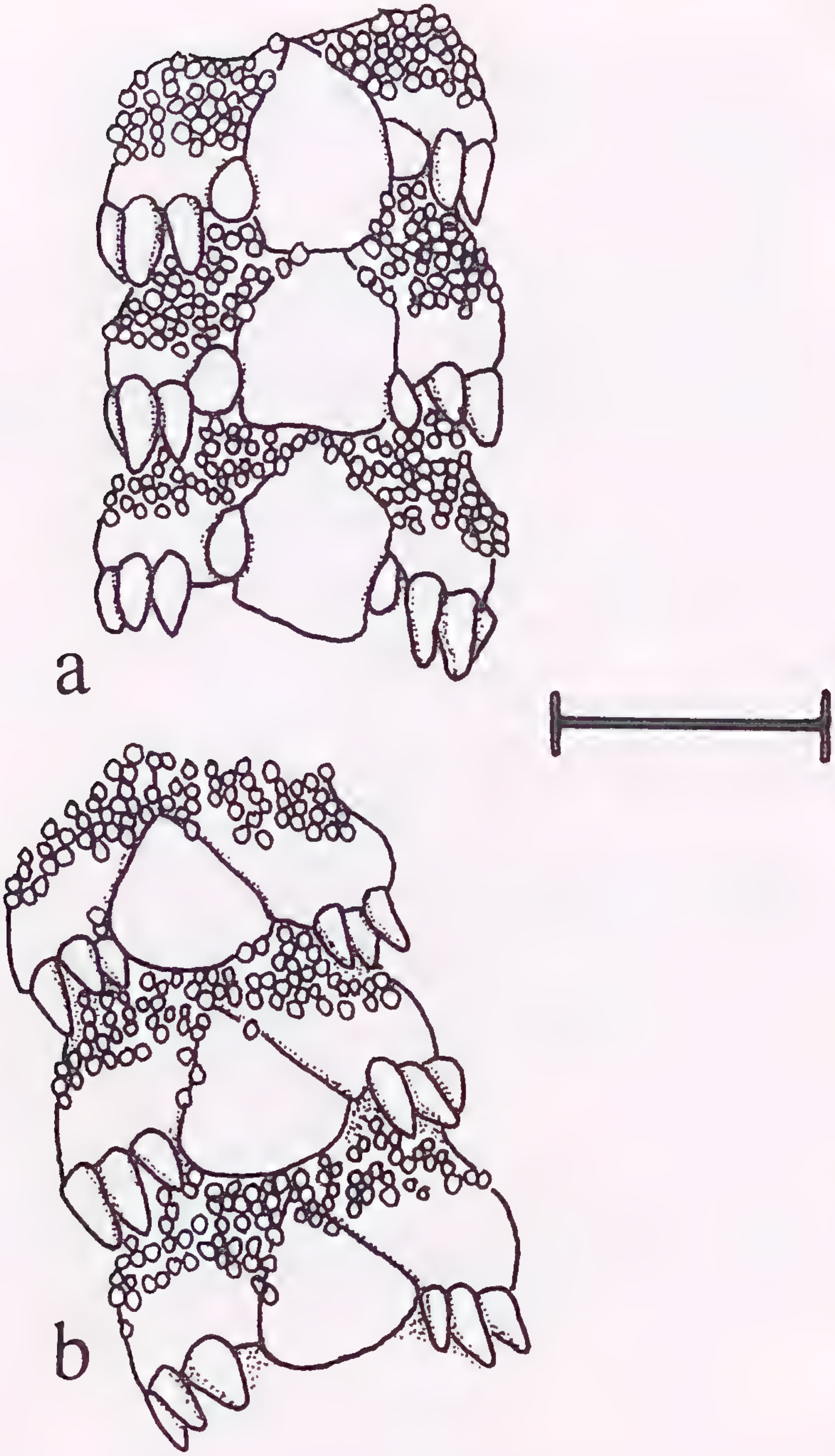


Fig. 6a. *Ophiodyscrita pacifica* (Murakami). Ventral surface of the arm, segments 5-8. 6b. Dorsal surface of the arm, segments 5-8. Scale represents 1.0 mm.

### **Ophiopeza spinosa** (Ljungman)

*Ophiarachna spinosum* Ljungman, 1867:305.
*Ophiopezella spinosa.* — H. L. Clark, 1921: 141; 1946:258.
*Ophiopeza spinosa.* — A. M. Clark & Rowe, 1971:90, 127, text-fig. 44e. — Gibbs *et al.*, 1976: 130.

MATERIAL

Station 1-2 (J.8881); Station 6-2 (J.8882).

The present record represents an extension of range southward from the northern part of the Great Barrier Reef.

Live colour notes with one of the Station 1 specimens describe the brittlestar as cream with faint brown cross-bands on the dorsal arm surface. The dried material is similarly pigmented.

### **Ophiopsammus yoldii** (Lütken)

*Ophiopeza yoldii* Lütken, 1856:98.
*Pectinura yoldii.* — H. L. Clark, 1921:141; 1946:257.
*Ophiopsammus yoldii.* — A. M. Clark, 1968:317, fig. 9a, b. — A. M. Clark & Rowe, 1971:90, 127, pl. 21, figs. 7, 8. — Gibbs *et al.*, 1976:130.

MATERIAL

Station 6-2 (J.8889-8890).

Live colour notes for one specimen describe the disc and arms as cream and the arms broadly cross-banded with orange. In the dried specimen, the orange cross-bands have faded to brown.

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## ACKNOWLEDGEMENTS

The author wishes to thank the curator of Echinoderms at the Australian Museum, Dr F. W. E. Rowe, for the opportunity to study this collection. Thanks are also due to Miss A. M. Clark, British Museum (Natural History), London and to Dr R. Woolacott, Museum of Comparative Zoology, Harvard, for the loan of type material. Preliminary identifications of the Swain Reefs echinoderms were made by Miss C. J. Cannon in 1974. During this study, the author was supported by a Queen's Fellowship in Marine Biology.

**Table 1. Stations sampled by the Swain Reefs Expedition, 1962.**

| Station | Location, depth and deposit |
|---|---|
| 1. | Whole of reef and sand flats adjacent to base camp, N. W. end of Gillett Cay (21° 43'S:152° 25'E) |
| 2. | Reef crest at Price Cay, approximately 3 miles S.E. of Gillett Cay |
| 3. | Dredgings from coral sand, 5m, lagoon of Gillett Cay, about 1 mile E. of cay* |
| 4. | Dredgings from 36.5m, off Gillett Cay adjacent to Station 3* |
| 5. | Dredgings from 27.5-36.5 m, off Gillett Cay, in vicinity of anchorage* |
| 6. | Dredgings from 64-73 m, off Gillett Cay, approximately 2 miles N.E. of anchorage* |
| 7. | Beach at Thomas Cay, approximately 8 miles N.W. of Gillett Cay |
| 8. | Beach and adjacent reef of Capre Cay (22° 09'S:152° 25'E) including shallow dead-coral area close to cay, reef-flat and reef-crest |

*dredgings taken with either a metre triangle dredge or a large wire-mesh dredge.

Manuscript accepted for publication 14 December, 1978.

# SPIDER CRABS OF THE FAMILY HYMENOSOMATIDAE (CRUSTACEA; BRACHYURA) WITH PARTICULAR REFERENCE TO AUSTRALIAN SPECIES: SYSTEMATICS AND BIOLOGY

-7 JUN [illegible]
OF VICTORIA

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## SUMMARY

The family Hymenosomatidae is revised as a result of discovering a large range of species in Australia. Three new genera and seven new species are described from the Australasian region. The genera *Rhynchoplax* Stimpson, *Neorhynchoplax* Sakai and *Cyclohombronia* Melrose are relegated to junior synonomy of *Halicarcinus* White, *Elamenopsis* A. Milne Edwards and *Hymenosoma* Desmarest, respectively. *Trigonoplax* H. Milne Edwards, treated by some authors as a subgenus of *Elamena* H. Milne Edwards, is given generic status on the basis of crab and larval morphology. The family now consists of ten genera and sixty-four species; seven genera, including all multispecific genera, and twenty-two species occur in Australia. An annotated key to all genera and species is provided. Diagnostic features for hymenosomatid larvae are given and larval morphology is considered in resolving several taxonomic problems. Absence of a megalopa larva is a notable family feature. Data on the life-cycles, reproduction, behaviour and ecology of hymenosomatids are reviewed. Fecundity is limited by the small sizes of these crabs and some females show morphological adaptations to increase shallow coastal waters and there has been a number of independent invasions of low fecundity by increasing larval survival. The majority of hymenosomatid species occur in shallow coastal waters and there have been a number of independent invasions of low salinity habitats. Twenty-four species, from six genera, occur in fresh and brackish water. Hymenosomatids reach high densities in some habitats and frequently occur in fish gut contents at various localities: they may play significant roles in some food webs. Most hymenosomatid species occur in the tropical and sub-tropical shelf waters of the Indo-West Pacific region and adjacent inland waters. Because they are inconspicuous, geographical distributions of many species are poorly known; the Indo-Malayan Region, which is central to their distribution, is particularly poorly collected.

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## INTRODUCTION

The family Hymenosomatidae consists of small to very small spider crabs (maximum carapace width 3-26 mm), which occur mainly in the Indo-West Pacific region. Major revisions of the family have been undertaken by Kemp (1917), Tesch (1918) and Sakai (1938). Each of these authors was disadvantaged by having access to a limited range of hymenosomatid species and the taxonomy of the family is unstable at the generic level. Kemp (1917) had mainly Indian species and a number of genera were not represented in his material. Tesch (1918) examined five species in the Leyden and Amsterdam Museums and two species from the "Siboga" expedition. Sakai (1938) had access to six Japanese species. There was a further major study of hymenosomatid taxonomy by Melrose (nee Gordon) (1975), which was limited to New Zealand hymenosomatids, consisting of fourteen species in four genera. Melrose (1975) was based on a thesis, Gordon (1966), part of which was published as keys to New Zealand Hymenosomatidae (Melrose, 1968). This study by Melrose clarified the confused literature on New Zealand species and was particularly helpful in considering the Australian hymenosomatids.

In contrast to the substantial, though confused, literature on New Zealand hymenosomatids, knowledge of the Australian species has suffered most from neglect. There has been only one attempt at a comprehensive survey of Australian species:

Haswell (1882c) included five species in his catalogue of Australian "stalk- and sessile-eyed" Crustacea. Two of these species, *Hymenosoma planatum* (Fabricius) and *H. varium* (Dana) (Haswell considered that all hymenosomatids belonged in one genus, *Hymenosoma*), are now known to be invalid records and one species, *H. krefftii* (Hess), has not been reported since. Hymenosomatids were also included in three later studies of crustacean faunas of particular regions of Australia. Fulton and Grant (1906b) listed five species from Victoria; Hale (1927) and Griffin (1972) gave the same five species for South Australia and southern-S.E. Australia, respectively. In a study of the physiology and ecology of Australian species of *Halicarcinus* White, Lucas (1968) included a review of their taxonomy and gave eight *Halicarcinus* species known to occur in Australia. Thus, after Lucas (1968), eleven hymenosomatid species were known to occur in Australia: eight *Halicarcinus* species, two *Elamena* species and one *Trigonoplax* species. All except *Elamena truncata* (Stimpson) were from southern (temperate) Australia.

Examination of the Australian museum collections and other collections from northern (tropical) Australia during this study revealed that there are many unrecorded and undescribed hymenosomatid species in Australia and that all the multispecific genera of Hymenosomatidae are represented by species in Australia. For the first time there was the opportunity to review the taxonomy of the family with a representative range of species at hand. A review of all the biological data on hymenosomatids was also undertaken to make a comprehensive study of the family.

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## PART A, SYSTEMATICS

### MATERIAL, METHODS AND ABBREVIATIONS

Most of the specimens examined in this study are kept in the six major Australian museums. Unless otherwise indicated, specimens are preserved in alcohol. Since some preserved specimens shed limbs with any handling, many of the specimens have detached chelipeds and walking legs. Diagnoses and descriptions are based on mature females and large males unless otherwise indicated. Allometric growth occurs in these species: carapace width to length ratio changes during growth, and rostrum, eyes and walking legs usually become relatively smaller. The onset of maturity in females is marked by an abrupt expansion of the abdomen, curvature of the abdomen to create a cavity between the abdomen and sternum (the abdominosternal or brood cavity), and development of the pleopods. (These comments do not apply to *Elamenopsis* females.) Males also show morphological changes at a late instar, but they may be sexually mature before this instar. Hence "large" is used instead of "mature" in describing late-instar males. The morphological changes in large males usually take the form of one or more of the following: elongation of the rostrum, elongation of body spines, and elongation and expansion of the chelipeds, compared to small males and females.

Measurements were made with vernier calipers or an eyepiece scale according to size. The general measure of size is given as maximum carapace width, which is usually about the level of the posterior lateral carapace angles. The rostrum is included in measurements of carapace length unless otherwise indicated. Walking leg length is measured from the longest leg, usually the second walking leg.

The terminology used in descriptions follows Melrose (1968, 1975) and is illustrated in Fig. 1.

The following abbreviations are used in giving details of specimens examined:

| | |
|---|---|
| im., | immature |
| juv., | juvenile (could not be sexed) |
| ov., | ovigerous |
| AHF, | Allan Hancock Foundation, California, U.S.A. |
| AM, | Australian Museum, Sydney, N.S.W. |
| BM, | British Museum (Natural History), London, U.K. |
| CSIRO, | Moreton Bay Collection, CSIRO Fisheries and Oceanography, Cronulla, N.S.W. |
| IFCT, | Inland Fisheries Commission of Tasmania, Tasmania |
| JCU, | School of Biological Sciences, James Cook University, Queensland. |
| MHN, | Muséum d'Histoire Naturelle, Paris, France |
| NMV, | National Museum of Victoria, Melbourne, Victoria |
| QM, | Queensland Museum, Brisbane, Queensland. |
| SAM, | South Australian Museum, Adelaide, South Australia. |
| TM, | Tasmanian Museum, Hobart, Tasmania. |
| WAM, | Western Australian Museum, Perth, Western Australia. |
| ZLKU, | Zoology Laboratory, Faculty of Agriculture, Kyushu University, Japan. |

## Family **HYMENOSOMATIDAE** MacLeay, 1838

Hymenosomidae MacLeay, 1838:68.— Alcock, 1900:285, 291.— Borradaile, 1907:480.— Rathbun, 1925:561.— Sakai, 1938-:193.— Garth, 1950:30.

Hymenosomatidae.— Stebbing, 1905:49.— Barnard, 1950:66-7.— Balss, 1957:1632.— Holthuis, 1968:109-10.— Melrose, 1975:7-8.

See Rathbun (1925) for other synonyms of the family name.

DIAGNOSIS: Cephalothorax thin dorso-ventrally, cuticle not heavily calcified, without hooked setae; dorsal carapace surface flat or nearly flat, often with strong gastro-cardiac groove and contiguous grooves; without orbits or with very incomplete orbits, eyes exposed and little retractile; antennular fossae shallow and poorly defined; antennae fused with epistome (when present), second segment slender; ischium of 3rd maxillipeds well developed, palp articulating near antero-lateral angle of merus; chelipeds not longer than twice carapace width in females and most males, fingers not bent at an angle to palm; male and female abdomens with not more than five segments, excluding telson; male genital apertures sternal; female genital apertures on sternites of 1st walking legs (2nd pereiopods). (Based on Alcock (1900), Borradaile (1907), Barnard (1950) and Balss (1957).)

REMARKS: Hymenosomatids differ from the usual malacostracan pattern of six abdominal segments in never having more than five abdominal segments. Since in female hymenosomatids pleopods occur on abdominal segments 2-5, which are followed by the telson, it appears that the 6th abdominal segment has been lost or obscured by fusion with segment 5 or the telson. Evidence for fusion of the 6th segment and telson is the unusually long proximal portion of the telson in hymenosomatid zoeae. The pattern of five abdominal segments is regarded as normal for hymenosomatids and references to fused and unfused abdomens refer to this basic condition of five segments and telson.

The name of this family (Hymenosomidae versus Hymenosomatidae), the source of the name and the location of the family within Section Brachyura, Order Decapoda, have varied between authors. Recently, Holthuis (1968) found that the oldest known use of the family name was by MacLeay (1838) and Holthuis established that the grammatically correct version of the name is Hymenosomatidae.

Melrose (1975) traced the history of positioning the Family Hymenosomatidae within the Section Brachyura. The hymenosomatids were initially regarded as catometopous crabs; then, later, they were placed in the Superfamily Oxyrhyncha. This is not accepted by some authors as an ideal location. For example, Aikawa (1929), Gurney (1938, 1942) and Wear (1967) saw more affinities of hymenosomatid larvae with larvae of Pinnotheridae (Brachyrhyncha) and Leucosiidae (Oxystomata) than with the larvae of the other oxyrhynchan families; while Richer de Forges (1976, 1977) considered that positioning of the Hymenosomatidae with the catometopous crabs should be reconsidered, particularly in view of the positions of genital apertures and larval morphology. Now Guinot (1977) has proposed a completely new classification of the Brachyura based on positions of genital apertures. In her classification the Hymenosomatidae are included in a Superfamily, Hymenosomatidea, which with six other superfamilies, Gecarcinoidea, Grapsoidea, Mictyroidea, Pinnotheroidea, Hexapodoidea and Ocypodoidea, is in a new taxon, Thoracotremata Guinot, 1977. The Thoracotremata have male and female sternal openings. As well as recognising the affinity of hymenosomatids with catometopous crabs, seen by some previous authors, Guinot's classification expresses the lack of close affinity with any other brachyuran family by placing the hymenosomatids in a separate superfamily.

## LARVAL CHARACTERS OF HYMENOSOMATIDAE AND GENERA

Diagnosis of the larval morphology of the family Hymenosomatidae, based on Wear (1967) and Lucas (1971):—telson elongate trapezoidal, wider anteriorly; telson-fork short and straight, with three pairs of close-set spines; 2nd maxillae with single coxal and basial endites, coxal endite vestigial, with a single seta or, less commonly, with two setae; antennae simple, varying from inconspicuous blunt lobes to conspicuous pointed lobes, pointed form with a fine basal hair or terminal spine which tends to be eccentric; abdomen of 5 segments with no traces of pleopods; with three zoeal stages and without pre-zoeal and megalopa stages.

The distinctive telson and telson fork of hymenosomatid larvae are the most useful characters for identifying these larvae in plankton samples.

There is much variation in the development of carapace spines within this family. In addition to the rostral spine, which is always present, mid-dorsal and inferior-lateral spines may also be present. The rostral spine varies from a short blunt lobe to an elongate spine, three times the length of the carapace. As a rule the hymenosomatid species occurring in brackish water have greater development of the larval carapacial spines than do the marine species.

The number of hymenosomatid species for which the larval morphology is known will be substantially increased with the publication of descriptions of most of the fourteen New Zealand species (R. G. Wear, pers. comm.). At this stage larval morphology is not known for enough species in most genera to give generic diagnoses. Details of larval morphology are known for the following species:—

*Hymenosoma* Desmarest: Broekhuysen (1955) figures lateral views of two larval stages of *H. orbiculare* Desmarest. The larvae have an elongate rostral spine and a mid-dorsal spine. The appendages are not detailed.

*Elamena* H. Milne Edwards: *E. mathaei* (Desmarest), described by Gurney (1938, 1942) and Al-Kholy (1959); *E. sindensis* Alcock by Prasad and Tampi (1957); *E. cristatipes* Gravely by Hashmi (1970); *E. producta* Kirk and *E. longirostris* Filhol by R. G. Wear (unpublished data); *E. abrolhensis* Gordon by Lucas (unpublished data). Sufficient species are now known to give a diagnosis for larvae of this genus:— globular carapace, without spines except for a short rostral spine; antennules and antennae short; 5th abdominal segment with prominent lateral expansions. From this diagnosis, the "Hymenozoea abdominalis" of Aikawa (1933) is identified as *E. truncata* (Stimpson), since this is the only *Elamena* species occurring in Japan.

*Halicarcinus* White: *H. messor* (Stimpson) described by Aikawa (1929) and Muraoka (1977); *H. coralicola* (Rathbun) described by Aikawa (1929); *H. varius* (Dana) figured by Wear (1965); *H. cookii* (Filhol) figured by Melrose (1975); *H. planatus* (Fabricius) described by Boschi, Scelzo and Goldstein (1969) and Richer de Forges (1976, 1977); *H. ovatus* Stimpson and *H. rostratus* (Haswell) described by Lucas (1971); *H. orientalis* Sakai by Muraoka (1977); *H. afecundus* n.sp. has large eggs, indicating abbreviated larval development. Larvae of this genus have globular carapaces, although the rostral spine may be of moderate length and there may be small spines on the inferior-lateral margins of the carapace.

*Trigonoplax* H. Milne Edwards: Aikawa (1929) described a larva of *T. unguiformis* (de Haan). The rostrum, antennules and antennae are of moderate length and the abdomen has no lateral expansions. The larva of this *Trigonoplax* species is unlike the larvae of *Elamena* species. Larval morphology does not support treatment of *Trigonoplax* as a subgenus of *Elamena*, e.g. by Alcock (1900), Kemp (1917) and Gordon (1940).

*Elamenopsis* A. Milne Edwards: *E. lineata* A. Milne Edwards has been studied by Lucas (unpublished data); *E. bovis* (Barnard) has suppressed larval development — Barnard (1950) described a female with thirteen 1 mm juveniles in its abdominosternal cavity; a freshwater species, *E. kempi* (Chopra and Das), probably has suppressed larval development — Abele (1972) described larger than normal eggs on ovigerous females. The larvae of *E. lineata* are striking, with very long mid-dorsal and rostral spines, two and three times the carapace length, respectively. Another feature of *E. lineata* larvae is the presence of two setae (not one) on the coxal endite of the 2nd maxilla.

*Amarinus* n.gen.: Lucas (1971) described larvae of *A. laevis* (Targioni Tozzetti) and *A. paralacustris* (Lucas); *A. lacustris* (Chilton) and *A. angelicus* (Holthuis) have no free larval stages (Lucas, 1971; J. C. Yaldwyn, pers. comm.). The larvae of *A. laevis* and *A. paralacustris* have well-developed carapace spines: rostral and inferior-lateral (both species) and mid-dorsal (*A. laevis* only) spines are present.

*Neohymenicus* n.gen.: Larvae of *N. pubescens* (Dana) have four short carapace spines and an abdomen with a laterally expanded 5th segment (Wear, 1968).

Larvae have not been described in three monospecific genera, *Hymenicoides* Kemp, *Halimena* Melrose and *Halicarcinides* n.gen.

## ANNOTATED KEY TO ALL GENERA, SPECIES AND INFRASPECIES OF HYMENOSOMATIDAE

The page number in brackets following each generic name in the key refers to further treatment of the genus in this text. After each species name in the key the following data are provided: size range (carapace width) of mature females, or other specimens as indicated; known geographical distribution; brief habitat details, where available; major references giving descriptions and figures of the species; comments on the species, including major synonyms; page number of further treatment in this text (Australian species).

Many of the non-Australian species of Hymenosomatidae were not examined during this study and the characters used in the key are derived from published descriptions.

| | | |
|---|---|---|
| 1 | Rostrum present; carapace of various forms ....................................... | 2 |
| — | Rostrum absent; carapace almost circular (two rare species only) ......... | 11 |
| 2(1) | Rostrum continuous with dorsal carapace surface, not separated by a ridge or groove; rostrum triangular or truncated; dorsal carapace surface without grooves except for a faint gastro-cardiac groove in some species | 3 |
| — | Rostrum separated from the dorsal carapace surface by a ridge or groove or both; rostrum of various forms; dorsal carapace surface usually with a distinct gastro-cardiac groove and contiguous grooves ....................... | 4 |
| 3(2) | Carapace, with rostrum, approximately triangular; Milne Edwards apertures fused laterally for more than half their length (see Fig. 5F) ....... *Trigonoplax* H. Milne Edwards, 1853 ... (p.186) ...................... | 12 |
| — | Carapace, with rostrum, polygonal to pear-shaped; Milne Edwards apertures not fused laterally for more than half their length ...... *Elamena* H. Milne Edwards, 1837 ... (p.170) .................................................. | 14 |
| 4(2) | Epistome present.................................................................................. | 5 |
| — | Epistome absent ...... *Hymenosoma* Desmarest, 1825 ... (p.166) ............ | 67 |
| 5(4) | Dorsal carapace surface with a distinct gastro-cardiac groove and contiguous grooves .................................................................................. | 6 |
| | Dorsal carapace surface without distinct grooves.............................. | 10 |
| 6(5) | 3rd maxillipeds narrow, not covering three-quarters of mouth-field, ischium much shorter than merus along lateral edge; with fused segments in male or female abdomen or both ... *Elamenopsis* A. Milne Edwards, 1873 ... (p.190) ......................................................................... | 26 |
| — | 3rd maxillipeds broad, covering three-quarters or more of mouth-field, ischium not much shorter than merus along lateral edge; usually without fused segments in male and female abdomens.................................. | 7 |
| 7(6) | Dactyli of walking legs with one or two rows of teeth .....*Halicarcinus* White, 1846 ... (p.176) .................................................................. | 44 |

— Dactyli of walking legs without teeth or with one or two subterminal teeth . 8

8(7) Rostrum distinctly trilobate ..... *Halicarcinus* White, 1846 ... (p.176) ....... 44

— Rostrum not distinctly trilobate, rostrum triangular to spade-shaped..... 9

9(8) Rostrum more triangular than spade-shaped; male 1st pleopod strongly curved, with a single row of long setae subterminally; gastric region of dorsal carapace surface strongly outlined by grooves extending to base of rostrum, gastric region much more indicated by grooves than other regions of carapace .... *Neohymenicus* n.gen. ... (p.208) .(monospecific)

*N. pubescens* (Dana, 1851); 4-8 mm; New Zealand; *Sargassum*, coralline algae turf and rock crevices, sheltered littoral and sublittoral to 11 m; Melrose 1975: 77-84, figs. 36-40.

— Rostrum more spade-shaped than triangular; male 1st pleopod little curved, not with a single row of long setae subterminally; gastric region of dorsal carapace surface not more strongly outlined by grooves than other carapace regions .... *Amarinus* n.gen. ...(p.198) ................................ 61

10(5) 3rd maxillipeds narrow, well separated medially .... *Hymenosoma* Desmarest, 1825 ...(p.166)............................................................ 67

— 3rd maxillipeds broad, almost meeting medially .... *Halimena* Melrose, 1975 ...(p.197)..............................................................(monospecific)

*H. aotearoa* Melrose, 1975; 6 mm; New Zealand; on algae, littoral and sublittoral, to 91 m; Melrose 1975: 106-9, figs. 53-54.

11(1) 3rd maxillipeds narrow, well separated medially; palp of 3rd maxillipeds elongate, reaching down to posterior edge of mouth-frame ... *Hymenicoides* Kemp, 1917. (p.196) ..................................(monospecific)

*H. carteri* Kemp, 1917; 6 mm (large ♂); Hughli, R., N.E. India; brackish; Kemp 1917: 268-70, figs. 17-21.

— 3rd maxillipeds broad, almost meeting medially; palp of 3rd maxillipeds not elongate, not reaching near posterior edge of mouth-frame ... *Halicarcinides* n.gen ...... (p.206) ...................................(monospecific)

*H. nuytsi* (Hale, 1927); 4.9-5.8 mm; S.E. Australian mainland; littoral and sublittoral; Hale 1928: 98-9, fig. 22; page 207

12(3) Rostral keel deep, extending to tip of rostrum, generally visible dorsally; rostrum often strongly upturned .................................*T. spathulifera* n.sp.

8-14 mm; northern Australia; variable habitat, from littoral zone on coral reefs to 130 m; page 188.

— Rostral keel shallow, not extending near tip of rostrum, not visible dorsally; rostrum never strongly upturned....................................... 13

13(12) Carapace width to length ratio approximately 1.0, less than 1.1......................................................*T. longirostris* McCulloch, 1908

13-17 mm; southern Australia; sublittoral, to 20 m; Hale 1924: 70-1, fig. 1; Hale 1927: 120-1, fig. 118; page 187.

— Carapace width to length ratio greater than 1.1.*T. unguiformis* (de Haan, 1839)

13-17 mm; widespread Indo-West Pacific distribution, excluding Australia; sublittoral, to 100 m; Kemp 1917: 277-8, figs. 28, 29; Tesch 1918: 25-6; Sakai 1938: 201-2, pl. 20 fig. 4; shows some morphological variation over its range (see page 187).

14(3) Rostrum triangular; carapace, with rostrum, tending to be pear-shaped; carapace width often less than carapace length in large specimens; with or without rostral keel forming a distinct T-shape with rostrum rim in anterior view ("triangular" species) .................... 15

— Rostrum truncate and broad; carapace, with rostrum, tending to be polygonal; carapace width often greater than carapace length in large specimens; with rostral keel forming a distinct T-shape with rostrum rim in anterior view ("truncate" species) .................... 21

15(14) Rostral keel forming a distinct T-shape with rostrum rim in anterior view 16

— Rostral keel absent or not forming a distinct T-shape with rostrum rim in anterior view .................... 18

16(15) Posterior portion of rostral keel developed into a long spine projecting anteriorly and ventrally; posterior lateral angles of carapace with a spine or tubercle projecting dorsally (approximately dorsal to base of 2nd walking leg) .................... *E. longirostris* Filhol, 1885a

7.5-10 mm; New Zealand; sublittoral, 11 m-116 m, on substrates of mud and shell, and sand and small stones; Takeda and Miyake, 1969: 181-4, fig. 7; Melrose 1975: 93-4, fig. 45.

— Posterior portion of rostral keel not developed into a spine; posterior lateral angles of carapace without a spine or tubercle .................... 17

17(16) Carapace width usually greater than carapace length; pterygostomial lobe not prominent; male abdomen very broad at base; male 1st pleopod with two groups of subterminal setae .................... *E. gracilis* Borradaile, 1903

6 mm; Maldive Archipelago; coral reef; Borradaile 1903: 684-5, fig. 122*; Gordon 1940: 71-3, figs. 1c, 6a, 6d, 7d; *Gordon (1940) states that both cotypes which she examined were "considerably more narrowly triangular" than Borradaile's figure.

— Carapace width usually equal to or less than carapace length; pterygostomial lobe prominent; male abdomen moderately broad at base; male 1st pleopod with one group of subterminal setae .................... *E. sindensis* Alcock, 1900

6.6 mm (♂); India and Sri Lanka; Alcock 1900: 386; Alcock and McArdle: 1902, pl. 64 fig. 4; Gordon 1940: 66-7, fig. 4.

18(15) Anterior lateral angles of carapace very prominent; antero-lateral carapace borders at right angles to longitudinal body axis..... *E. umerata* n.sp.

2.8 mm; northern Australia; among sessile invertebrates, littoral, sublittoral; page 175.

— Anterior lateral angles of carapace not prominent, only slightly indicated; antero-lateral carapace borders not at right angles to longitudinal body axis........................................................ ..........................................19

19(18) Dactyli of walking legs with row of small teeth; rostrum parallel sided at base..............................................................................*E. cimex* Kemp, 1915

6.5 mm; Bay of Bengal and Madagascar; euryhaline marine or brackish; Kemp 1915: 216-18, figs. 4, 5, pl. 12 fig. 3; Barnard 1962: 239; Barnard's specimens differ from those of Kemp in the extent of teeth on dactyli of walking legs and also in type of habitat; there may be two species represented here.

— Dactyli of walking legs without a row of small teeth, but with one or two subterminal teeth; rostrum completely triangular, sides convergent from base ........................................................................................... 20

20(19) Abdomen of mature female relatively very large, broader than body and conspicuous laterally in dorsal view, pleopods extending laterally from abdomen; rostral keel absent; lobes in pterygostomial and subhepatic regions prominent and visible dorsally..................*E. gordonae* Monod, 1956

2.3-3.0 mm; western Africa, N.E. Australia; sublittoral, 18-40 m; Monod 1956: 469-72, figs. 629-37; page 174.

— Abdomen of mature female of normal size, not broader than body, not conspicuous laterally in dorsal view, pleopods not extending laterally from abdomen; rostral keel present as a small tooth; lobes in pterygostomial and subhepatic regions not prominent and not visible dorsally..................................................................*E. xavieri* Kemp, 1917

8.5 mm; Mandavi R., India; brackish; Kemp 1917: 275-7, figs. 24-27.

21(14) Male abdomen without fused segments, consisting of 6 pieces including telson; terminal border of telson of mature female convex (New Zealand species)........................................................................................ 22

— Male abdomen with segments 3 and 4 fused and suture obscure, consisting of 5 pieces including telson; terminal border of telson of mature female concave or truncate (not from New Zealand)............... 23

22(21) Merus of walking legs with a prominent acute tooth on distal edge; anterior lateral and posterior lateral carapace angles distinct; rostral keel deepest anteriorly...................................................*E. producta* Kirk, 1879

7-14.5 mm; New Zealand; under boulders in sandy or pebbly pools in mid to low littoral; Melrose 1975: 95-102, figs. 46-50, pl. 1B.

— Merus of walking legs with a small obtuse or barely acute tooth on distal edge; anterior lateral and posterior lateral carapace angles indistinct; rostral keel not deepest anteriorly, of uniform depth along its length..........................................................*E. momona* Melrose, 1975

4.5-9 mm; New Zealand; shallow sublittoral, oyster beds; Melrose 1975: 102-6, figs. 51, 52.

23(21) Dactyli of walking legs with a single subterminal tooth, dorsal margin of propodus strongly compressed to a ridge and finely serrated; dactylus of chela of large males without a large basal tooth ....*E. cristatipes* Gravely, 1927

5 mm; India; sublittoral; Gravely 1927: 150, pl. 21 fig. 24; Chopra and Das 1930: 425-8, figs. 11-15.

— Dactyli of walking legs usually with two subterminal teeth, dorsal margin of propodus not strongly compressed to a ridge and not finely serrated; dactylus of chela of large males with a large basal tooth...................... 24

24(23) Male 1st pleopod with narrow distal portion approximately C-shaped, with approximately 5 subterminal setae; posterior lateral angles of carapace usually rounded and not evident .......................*E. truncata* (Stimpson, 1858)

5.6-9.3 mm; Indo-West Pacific, northern Australia to Japan; coral reefs, coral rubble, weedy and rocky shores, littoral and shallow sublittoral; Sakai 1938: 201, pl. 20 fig. 3; Gordon (1940) considers "it is highly probable ... that more than one species is represented"; page 172.

— Male 1st pleopod with narrow distal portion approximately S-shaped due to recurvature at apex, 8-12 subterminal setae; posterior lateral angles of carapace evident as pointed obtuse angles ....................................... 25

25(24) Subterminal setae on male 1st pleopods elongate, reaching or nearly reaching thick basal portion of pleopod if turned down towards basal portion; rostral keel not meeting interantennal septum; postocular lobes with an indistinct tooth or with no tooth...........*E. mathaei* (Desmarest, 1825)

4.5-7 mm; Red Sea, S.E. Africa, Mauritius; marine shallow sublittoral (?); Gordon, 1940: 63-4, figs. 1a, 1b, 2, 3a-3c; Barnard 1950: 73-5, figs. 15g-o.

— Subterminal setae on male 1st pleopods not elongate, not nearly reaching thick basal portion of pleopod if turned down towards basal portion; rostral keel continuous with interantennal septum; postocular lobes with a small acute tooth.........................................*E. abrolhensis* Gordon, 1940

6.8-8.4 mm; southern Australia; on hard substrates, rock or limestone, in littoral or shallow sublittoral; Gordon 1940: 70-71, figs. 6b, 6c, 7a, 7c, 10a; page 173.

26(6) Dactyli of walking legs without teeth ............................................... 27

— Dactyli of walking legs with a subterminal tooth or a row of teeth........ 35

27(26) Rostrum consisting of a single deflexed lobe ................................... 28

— Rostrum trilobate, although lateral lobes may be partially fused with medial lobe and very short .......................................................... 29

28(27) Walking legs broad and laterally compressed; fused section of male abdomen tapering, not constricting abruptly; male 1st pleopod without a spine-like apex.......................................*E. lineata* A. Milne Edwards, 1873

3-4 mm; New Caledonia, northeastern Australia, Philippines; brackish, muddy substrates; Tesch 1918: 26-8, pl. 1 fig. 5; page 192.

— Walking legs not broad and laterally compressed; fused section of male abdomen constricting abruptly; male 1st pleopod with a spine-like apex..............................................*E. inermis* (Takeda and Miyake, 1971a)

3.6 mm; Palau Islands; fresh water; Takeda and Miyake 1971a: 1-7, fig. 1; the ♂ paratype is much smaller than the ♀ holotype and its 1st pleopods, figs. 1f, 1g, may be stouter than in larger males.

29(27) Dorsal carapace surface with one or four large tubercles, one tubercle occurring medially on gastric region ........... *E. tuberculata* (Chopra and Das, 1930).......................................................................................... 30

<5-7.2 mm; southern India and Sri Lanka; brackish; Chopra and Das 1930: 419-24, figs. 6-10; Pretzmann 1975: 607-8, pl. 1 figs. 1-5; the variety, *E. t.* var. *attenuipes,* which is sympatric with the *forma typica,* and the subspecies, *E. t. pageti* from Sri Lanka, differ in important features from the *forma typica* and may be separate species.

— Dorsal carapace surface without large tubercles ................................ 32

30(29) With three large tubercles on cardiac region of dorsal carapace surface 31

— Without tubercles on cardiac region of dorsal carapace surface ..................................................*E. tuberculata pageti* (Pretzmann, 1975)

31(30) Walking legs broad, propodus of 2nd walking leg ca. 4 X as long as broad .....................................*E. tuberculata tuberculata* (Chopra and Das, 1930)

— Walking legs not broad, propodus of 2nd walking leg ca. 6 X as long as broad ................*E. tuberculata* var. *attenuipes* (Chopra and Das, 1930)

32(29) Walking legs broad and laterally compressed; lateral lobes of rostrum broad, short to very short, and obtuse ............................................ 33

— Walking legs slender; lateral lobes of rostrum narrow, short and acute. 34

33(32) Medial rostral lobe almost square, a little longer than broad; deflexed; carapace nearly circular.......................................*E. demeloi* (Kemp, 1917)

4.4 mm (♂); Goa, India; brackish, under stones on mud; Kemp 1917: 258-60, figs. 6-9.

— Medial rostral lobe triangular, not deflexed; carapace oval-octagonal, broader than long ..............................................*E. ariakensis* (Sakaï, 1969)

3.5 mm; Nagasaki Prefecture, Japan; commensal with holothurian, *Protankyra bidentata,* on mud flats; Sakai 1969: 250-51, figs. 2, 3; Sakai 1976: 150-1, figs. 79, 80a-d, pl. 47 fig. 1.

34(32) Rostrum consisting of three rounded lobes, fused at base; posterior lateral angles of carapace with a small acute tooth (approximately above base of 1st walking leg) .......................................*E. sinensis* (Shen, 1932)

2.3 mm (♂); Shantung Peninsula, China; littoral, under stones on mud flats and attached to echinoids; Shen 1932: 58-62, figs. 33-36, pl. 2 fig. 7.

— Rostrum consisting of three spine-like lobes, well separated, not fused at base; posterior lateral angles of carapace without a tooth...*E. aspinifera* n.sp.

3 mm; northeastern Australia; brackish-marine, muddy substrates; page 195.

35(26) Rostrum consisting of a single lobe, a pointed horizontal lobe approximately twice as long as wide.........................*E. nasalis* (Kemp, 1917)

4 mm; West Bengal, India; brackish; Kemp 1917: 265-7, figs. 12-15.

— Rostrum trilobate .......................................................................... 36

36(35) Posterior lateral angles of carapace with a spine below carapace rim (approximately dorsal to base of 1st walking leg) .............................. 37

— Posterior lateral angles of carapace without a spine .......................... 40

37(36) Rostral lobes fused at base; dactyli of walking legs 2-4 with a row of small teeth; antero-lateral borders of carapace with one or two short teeth ... 38

— Rostral lobes not fused at base, lateral lobes well separated from medial lobe; dactyli of walking legs without a row of teeth, with a subterminal tooth; antero-lateral borders of carapace without teeth ................................................................*E. octagonalis* (Kemp, 1917)

2.5-3 mm; Goa, India, and Moreton Bay, Queensland, Australia; littoral, muddy substrates; Kemp 1917: 256-8, fig. 5; page 193.

38(37) Medial lobe of rostrum much longer than broad; male telson subequal in length and breadth ...................................................................... 39

— Medial lobe of rostrum almost as broad as long; male telson distinctly longer than broad.....................................*E. kempi* (Chopra and Das, 1930)

4-6 mm; Basra, Iraq, and Panama Canal, Central America; fresh water, on plants; Chopra and Das 1930: 416-19, figs. 2-5; Abele 1972: 211-15, figs. 1-3; Abele suggests that *E. kempi* was introduced into the Panama Canal with the water plant *Hydrilla verticillata*, after 1939.

39(38) Carapace length, excluding rostrum, to width ratio approximately 1.1:1; antero-lateral borders of carapace with two small teeth; fingers of chelae of large males not widely gaping at base......... *E. woodmasoni* (Alcock, 1900)

6 mm (♂); Andaman Islands and West Bengal, India; marine (?); Alcock 1900: 388; Alcock and McArdle 1902: pl. 64 fig. 3; Kemp 1917: 252-3, 255-6, fig. 4a-c.

— Carapace length, excluding rostrum, to width ratio approximately 1:1; antero-lateral borders of carapace with one small tooth; fingers of chelae of large males widely gaping at base........................*E. alcocki* (Kemp, 1917)

4 mm; west coast, India; brackish, muddy substrates and on fouling organisms; Kemp 1917: 253-6, figs. 3, 4d-g; Chopra and Das 1930: 414-16, fig. 1; Abele 1972: 215, figs 2A, 3A.

40(36) Dactyli of walking legs with a row of teeth; lateral lobes of rostrum not widely separated from medial lobe, not pointing inward ..................... 41

— Dactyli of walking legs without a row of teeth, with one subterminal tooth; lateral lobes of rostrum widely separated from medial lobe, pointing inward ..........................................................................*E. torrensica* n.sp.

4.3 mm; Thursday Island, northern Australia; marine (?); page 194.

41(40) Rostrum consisting of three elongate spines, length of medial lobe of large male approximately one third of carapace length, excluding rostrum ........................................................*E. inachoides* (Alcock, 1900)

6 mm (♂); West Bengal, India; marine (?); Alcock 1900: 388-9; Alcock and McArdle 1902: pl. 65 fig. 1; only known from ♂ holotype.

— Rostrum not consisting of three elongate spines, at least medial lobe with rounded apex, length of medial lobe usually much less than one third of carapace length, excluding rostrum ............................................... 42

42(41) Branchiostegites with strong crest projecting dorsally and reaching higher than postero-lateral border of carapace; rostral lobes not fused or barely fused at base in dorsal view ..................*E. introversa* (Kemp, 1917)

<5.4 mm (♂); Kiangsu Province, China; fresh water; Kemp 1917: 262-4, fig.11.

— Branchiostegites without a strong crest projecting dorsally; rostral lobes substantially fused at base in dorsal view........................................... 43

43(42) Fingers of male chelae gaping at base, meeting only in distal third, without teeth; male telson much longer than broad; with an obtuse tooth at anterior lateral angles of carapace; sometimes with very prominent spines on postocular lobes ...........................................*E. bovis* (Barnard, 1947)

<5.5 mm; South Africa; sublittoral to 68 m, brackish; Barnard 1950: 72-3, fig. 15c-f; considering the range of habitats and morphological variation described by Barnard (1950), several taxa may be represented here; without free larval development.

— Fingers of male chelae meeting along most of their length, with approximately 5 teeth (each?); male telson slightly shorter than broad; without a tooth at anterior lateral angles of carapace; never with very prominent spines on postocular lobes......................*E. exigua* (Kemp, 1917)

3.3 mm; Thailand; brackish; Kemp 1917: 260-2, fig. 10.

44(7&8) Rostrum distinctly trilobate or tridentate, concavities between lobes reaching almost to carapace rim.................................................... 45

— Rostrum not distinctly trilobate or tridentate, concavities between lobes not reaching near carapace rim ..................................................... 53

45(44) Medial rostral lobe much longer than lateral lobes ............................ 53

— Medial rostral lobe subequal with or shorter than lateral lobes ........... 46

46(45) Dactyli of walking legs with one or two rows of small teeth ................ 47

— Dactyli of walking legs without a row of small teeth, but with one or two subterminal teeth ...................................................................... 51

47(46) With an acute spine on lateral carapace walls or carapace rim at posterior lateral angle (approximately dorsal to base of 1st walking leg); rostral lobes arising at level of carapace rim or slightly below............................... 48

— Without an acute spine on lateral carapace walls or carapace rim at posterior lateral angle; rostral lobes arising well below carapace rim ....................................................*H. innominatus* Richardson, 1949b

6.5-15.5 mm; New Zealand, Chatham Islands, Tasmania; associated with mussels, *Perna canaliculus,* in littoral zone (Melrose, 1975); Melrose 1975:

26-34, figs. 5-11, pl. 1C-F; specimens of *H. innominatus* from New Zealand have generally been called *H. planatus* (Fabricius), however this latter species occurs south of New Zealand (Melrose, 1975); page 182.

48(47) Rostral lobes extending well beyond eyes — thin and well separated ........................................................................*H. tongi* Melrose, 1975

6.5 mm; New Zealand; deep sublittoral, to 500 m; Melrose 1975: 88-92, figs. 43, 44.

— Rostral lobes not extending beyond eyes; *or* if extending beyond eyes, rostral lobes moderately broad and set close together ........................ 49

49(48) Medial rostral lobe shortest, lateral lobes sloping downward; anterior lateral angles of carapace not marked by angles in carapace rim ..............................................................*H. planatus* (Fabricius, 1775)

3.5-6 mm (Chile), 8-11 mm (Strait of Magellan), 8-19 mm (Auckland Islands), 12-14 mm (Kerguelen Island); circum-polar subantarctic; under rocks and among fronds of algae *Macrocystis pyrifera* in littoral zone, in sublittoral to 270 m; Garth 1958: 31-5, fig. 1, pl. 1; Melrose 1975: 34-9, figs. 12, 13; Richer de Forges 1977: 74-81, figs. 1-5.

— Medial rostral lobe slightly longer than lateral lobes, lateral lobes not sloping downward; anterior lateral angles of carapace marked by obtuse angles in carapace rim .................................................................. 50

50(49) Large males with basal tooth on dactylus of chela; concavities between rostral lobes usually at least reaching carapace rim; rostrum often arising slightly below level of carapace rim; antero-lateral carapace borders slightly concave to straight ..................................*H. ovatus* Stimpson, 1858

4-10 mm, mostly 5-6 mm; southern Australia; rocky substrates, among mussels and algae, littoral and sublittoral, to 60 m; Hale 1927: 117, fig. 113; Melrose 1975: 39-44, figs. 14, 15; very variable species (see p.179), Hale and Melrose do not show the range of variation; page 179.

— Males without basal tooth on dactylus of chela; concavities between rostral lobes not reaching carapace rim; rostrum at level of carapace rim; antero-lateral carapace border concave ....................*H. cookii* (Filhol, 1885b)

3-8.5 mm; New Zealand; on algal substrates, littoral and shallow sublittoral; Melrose 1975: 44-59, figs. 1-4, 16-18, 21, pl. 2.

51(46) Lateral lobes of rostrum distinctly longer and broader than medial lobe ..........................................................................*H. afecundus* n.sp.

5.4 mm; Great Barrier Reef, Australia (one locality); marine, sublittoral; page 185.

— Lateral lobes of rostrum not longer and broader than medial lobe........ 52

52(51) With an acute spine on lateral carapace walls, approximately dorsal to base of 1st walking leg ...............................*H. minutus* (A. Milne Edwards, 1873)

5.4 mm; New Caledonia; marine; A. Milne Edwards 1873: 324, pl. 18 fig. 5; Takeda and Nunomura 1976: 65-6, fig. 2.

— Without an acute spine on lateral carapace walls.......*H. orientalis* Sakai, 1932

4-6 mm (?); Japan; shallow beaches, under stones and weeds (Sakai); Sakai 1932: 42-3, fig. 1, pl. 2 fig. 1; Sakai 1938: 195, pl. 20 fig. 1.

53(44 & 45) Rostrum extending beyond eyes, deflexed or upturned, not forming a short, almost horizontal platform .................................................. 54

— Rostrum not extending beyond eyes, forming a short, almost horizontal platform ............................................................*H. varius* (Dana, 1851)

4-10 mm; New Zealand; sheltered littoral and sublittoral to 18 m, on stones, algae, *Zostera* or buried in sand; Melrose 1975: 59-68, figs. 25-28, pl. 2E; rostrum variable in form, which has caused confusion with *H. cookii* (see Melrose 1975: 66).

54(53) With an acute tooth or spine on lateral carapace walls at posterior lateral angles of carapace (approximately dorsal to base of 1st walking leg) ..... 55

— Without an acute tooth or spine on lateral carapace walls at posterior lateral angles of carapace .......................................................... 58

55(54) Medial lobe of rostrum spatuliform, broadest about halfway along its length and broadly rounded apically..................*H. messor* (Stimpson, 1858)

5 mm (♂); Japan; littoral zone of rocky beaches, under stones or in algae; Sakai 1938: 197-8, fig. 1, pl. 20 fig. 2; Sakai 1965: 63, fig. 9, pl. 25 fig. 2; previously known as *Rhynchoplax messor.*

— Medial lobe of rostrum styliform, broadest at base and tapering to apex. 56

56(55) Rostrum with one or more long hairs arising from apex; abdomen of mature female broader than body, conspicuous laterally in dorsal view, with segments 3 and 4 fused; walking legs moderately stout ....................................................*H. hondai* (Takeda and Miyake, 1971b)

2.6 mm; Ryukyu Islands, Japan, and Great Barrier Reef, Australia; coral rubble and green algae on coral reef flats, littoral; Takeda and Miyake 1971b: 168-70, fig. 3; page 183.

— Rostrum without long hairs arising from apex; abdomen of mature female not broader than body, not conspicuous laterally in dorsal view, without fused segments; walking legs slender ............................................. 57

57(56) Lateral margins of rostrum fringed with setae; anterior lateral carapace angles with an obtuse tooth; posterior lateral carapace angles with an acute tooth ................................................*H. setirostris* (Stimpson, 1858)

4.4 mm; China, Japan; muddy and shelly substrates, sublittoral 25-110 m; Sakai 1938: 198-9, fig. 2; Sakai 1976: 148-9, figs. 76b, 77, pl. 46 fig. 3; previously known as *Rhynchoplax setirostris; = Halicarcinus yangi* Shen, 1932 (Sakai, 1965).

— Lateral margins of rostrum not fringed with setae; anterior lateral carapace angles without an obtuse tooth; posterior lateral carapace angles with an acute spine pointing vertically ..........................*H. rostratus* (Haswell, 1882a)

3-5.5 mm; southern Australia; often on algae, sublittoral, to 90 m; Hale 1927: 117-18, fig. 114; page 180.

58(54) Medial rostral lobe fringed with short setae along lateral edges; lateral rostral lobes terminating in an acute point........................................ 59

— Medial rostral lobe not fringed with short setae along lateral edges; lateral rostral lobes with rounded apex or completely fused with medial lobe . 60

59(58) Anterior lateral angles of carapace with an acute tooth; base of rostrum not fused with postocular lobes in a broad band above eyestalks; medial rostral lobe without long terminal hairs.............*H. coralicola* (Rathbun, 1909)

3.6 mm (♂); Japan, Taiwan, Singapore; coral reef, rocky substrates and algal holdfasts; littoral; Sakai 1938: 199-200; Sakai 1976: 144, figs. 76a, 78a-e, pl. 46 fig. 4; previously known as *Rhynchoplax coralicola;* = *Halicarcinus septentrionalis* Yokoya, 1928 (Sakai, 1965).

— Anterior lateral angles of carapace without an acute tooth; base of rostrum fused with postocular lobes in a broad band above eyestalks; medial rostral lobe with several long terminal hairs .................................................*H. keijibabai* (Takeda and Miyake, 1971b)

1.9 mm; New Caledonia; Takeda and Miyake 1971b: 165-8, figs. 1,2; abdomen of mature female broader than carapace and with pleopods extending beyond abdomen.

60(58) Rostrum approximately triangular, narrowing abruptly about half-way or further along its length where lateral lobes terminate, lateral lobes completely fused with medial lobe; body and legs not covered with long dense hairs...............................................*H. bedfordi* Montgomery, 1931

4-6.7 mm (Swan River), 3-4 mm (northern localities); northern Australia, but extending to Swan River on west coast; muddy substrates and algae, littoral and shallow sublittoral, euryhaline marine; Montgomery 1931: 425-6, pl. 27 figs. 3, 3a, 3b; page 181.

— Rostrum approximately spade-shaped, not narrowing abruptly along its length, terminally trilobate; body and legs covered with long hairs in large specimens ..........................................................*H. whitei* (Miers, 1876)

7-11.5 mm; New Zealand; littoral, sheltered marine and estuarine localities, among *Zostera* or buried in sand; Melrose 1975: 69-77, figs. 31-33, 35, pl. 1A.

61(9) Antero-lateral margins of carapace with a row of conspicuous teeth; walking legs with long, dense hairs; chelae of large males with dense hairs on posterior side of propodus ............................*A. woltereckii* (Balss, 1934)

11 mm (large ♂); Mindanao, Philippines; freshwater lake; Balss 1934: 181-3, figs. 3-5.

— Antero-lateral margins of carapace without a row of conspicuous teeth; walking legs without dense hairs; chelae of large males usually without dense hairs................................................................................. 62

62(61) With numerous thin spines (or spinules) on carapace margins, rostrum, pterygostomial regions, walking legs and chelipeds ........................................................*A. pilosus* (A. Milne Edwards, 1873)

26 mm (large ♂); New Caledonia; fresh water, sandy substrates; Milne Edwards 1873: 322-3, pl. 18 fig. 6; Holthuis 1968: 117-19, fig. 3.

— Without numerous thin spines on body and legs.............................. 63

63(62) Mature females generally greater than 10 mm; antennal spines acute and prominent; male 1st pleopods not tapering to a point, apex with a large blunt lobe and smaller curved lobe; chelae of large males with a pulvinus (a sac arising between the bases of the fingers) ..................................................*A. laevis* (Targioni Tozzetti, 1877)

10-18 mm; southern Australia; brackish water, estuaries; Montgomery 1931: 423-5, pl. 27 figs. 4, 4a; largest Australian hymenosomatid, readily distinguished from other Australian *Amarinus* n.gen. species by its size; generally known as *Halicarcinus australis* (Haswell) in previous literature; page 199.

— Mature females generally less than 10 mm; antennal spines small and obtuse; male 1st pleopods tapering to a point; chelae of large males without a pulvinus.................................................................................. 64

64(63) Rostrum strongly deflexed, almost vertical; orbits well separated from carapace rim by lateral extensions of rostum base ..........................................................*A. angelicus* (Holthuis, 1968)

8 mm; Southern Highlands, Papua-New Guinea; freshwater swamp; Holthuis 1968: 112-16, figs. 1, 2.

— Rostrum deflexed, but not near vertical; orbits usually reaching near to carapace rim........................................................................................ 65

65(64) Postocular lobes large, prominent in dorsal view, extending laterally along antero-lateral borders of carapace, and, with slightly deflexed rostrum, forming a shield across anterior of carapace .....................*A. latinasus* n.sp.

4 mm; North Queensland; brackish; page 205.

— Postocular lobes moderate sized, not prominent in dorsal view, not extending laterally along antero-lateral borders of carapace, and not forming a shield with rostrum..................................................... 66

66(65) Female genital apertures 0.4-0.5 mm wide, generally with a curved medial prominence (absent in North Queensland specimens); eggs less than 0.4 mm diameter; telson approximately 0.35 of total abdomen length in mature females...........................................*A. paralacustris* (Lucas, 1970)

5-8 mm; eastern Australia; brackish water, estuaries; Lucas 1970: 275-7, figs. 3c, 3e; *A. paralacustris* and *A. lacustris* can only be distinguished by egg size and the morphology of mature females; page 204.

— Female genital apertures 0.65-0.8 mm wide, without a curved medial prominence; eggs approximately 0.7 mm diameter; telson approximately 0.25 of total abdomen length in mature females.....*A. lacustris* (Chilton, 1882)

5-8 mm; southeastern Australasia; freshwater streams, freshwater and low salinity lakes; Melrose 1975: 84-8, figs. 41, 42; see comment above on *A. paralacustris;* page 201.

67(4 & 10) Epistome present, but short and narrow; without well defined grooves on dorsal carapace surface ...............................*H. depressum* Jacquinot, 1853

5-8 mm; New Zealand; littoral and sublittoral; Melrose 1975: 110-16, figs. 55-58; see p. 168 for comment on its inclusion in *Hymenosoma*.

— Epistome absent; with well defined grooves on dorsal carapace surface 68

68(67) Dactyli of walking legs with a row of fine teeth ................*H. hodgkini* n.sp.

4-7 mm; temperate eastern Australia; coastal, marine habitats; page 169.

— Dactyli of walking legs without teeth..............*H. orbiculare* Desmarest, 1825

6-24 mm; southern Africa; littoral and sublittoral, to 80 m, brackish and fresh water; Tesch 1918: 6-8, pl. 1 fig. 1; Barnard 1950: 68-71, fig. 15a, b; 1955: 19, fig. 5; very variable in morphology and habitat; this taxon probably represents several species, see page 168.

## **HYMENOSOMA** Desmarest, 1825

*Hymenosoma* Desmarest, 1825: 163 (type species, by designation of H. Milne Edwards (1837), *Hymenosoma orbiculare* Desmarest, 1825).

*Cyclohombronia* Melrose, 1975: 109-10 (type species, by original designation, *Hymenosoma depressa* Jacquinot, 1835).

DIAGNOSIS: Carapace elongate oval or subcircular, with anterior lateral and posterior lateral carapace angles not evident; dorsal carapace surface flat, with well defined or very weak grooves; rostrum triangular with rounded apex, separated from dorsal carapace surface by a groove, concave laterally, usually deflexed and shorter than eyes, with lateral portions extending over prominent eyestalks; epistome absent or narrow and very short; pterygostonial region plain; Milne Edwards apertures with wide gape; 3rd maxillipeds not meeting medially, narrow to moderately broad, ischium subequal or shorter than merus along lateral edge, palp large and conspicuous, epipodites conspicuous in wide Milne Edwards apertures; chelipeds stouter than walking legs, especially in large males, but not greatly inflated; walking legs slender or moderately stout, length 2 to 3 X carapace width, dactyli with a row of fine teeth or without teeth, with dense long setae; female abdomen without fused segments, with medial portions of segments 1-3 making a triangular or trapezoidal plate, segments 1 and 2 and part of 3 visible dorsally, abdomen not strongly convex laterally making abdominosternal cavity (brood cavity) broad and shallow; male abdomen without fused segments; male 1st pleopod with stout base, distal portion of moderate and relatively uniform thickness, distal portion almost straight or strongly curved, with at least one longitudinal row of long setae, terminating in a blunt apex with wide aperture, apex complex, with a dense zone of denticles or short setae.

SPECIES OF *HYMENOSOMA*:

| **Species** | **Distribution** |
|---|---|
| *H. orbiculare* Desmarest, 1825 | southern Africa and Zanzibar |
| *H. depressum* Jacquinot, 1853 | New Zealand |
| *H. hodgkini* n.sp. | eastern Australia |

REMARKS: *H. depressum* has been variously treated as congeneric with *H. orbiculare* and as a separate genus (see Melrose, 1975). Recent authors, commencing with Graham

TABLE 1. Morphological features in which *Hymenosoma orbiculare, H. depressum* and *H. hodgkini* differ. (+, present; −, absent).

| | Feature | H. orb. | H. depr. | H. hodg. |
|---|---|---|---|---|
| (a) | subcircular dorsal carapace | − | − | + |
| (b) | distinct grooves on dorsal carapace | + | − | + |
| (c) | rostrum reaching corneas of eyes | + | + | − |
| (d) | rostrum extending over eyestalks | + | − | + |
| (e) | very prominent postocular lobes | + | − | − |
| (f) | elongate eyestalks | + | − | + |
| (g) | antennal spines | − | + | − |
| (h) | epistome | − | + | − |
| (i) | very prominent mouth-frame angles | + | − | + |
| (j) | narrow 3rd maxillipeds | + | + | − |
| (k) | long slender walking legs | − | + | + |
| (l) | teeth on walking leg dactyli | − | − | + |
| (m) | posterior bulges on ♀ abdomen | − | + | + |
| (n) | arcuate ♀ telson | − | − | + |
| (o) | subtriangular ♂ abdomen | − | + | − |
| (p) | elongate seg. 5 in ♂ abdomen | − | − | + |
| (q) | distally curved ♂ 1st pleopod | − | + | − |
| (r) | intercalated plates in ♂ abdomen | − | − | + |

(1938), have favoured the latter course, calling the species *Hombronia depressa*. However, Gordon (1966) established that *Hombronia* Lucas is an invalid generic name for this taxon, since *Hombronia* is a junior synonym of *Halicarcinus*. Melrose (1975) proposed a new genus, *Cyclohombronia*, for *Hymenosoma depressum*. The reason for the separation is mainly that the New Zealand species has a very small epistome, while the type species, *H. orbiculare*, has no epistome. The epistome of *H. depressum* is, however, unlike any other hymenosomatid: it is so small that the green gland apertures are on the basal segments of the antennae. Melrose (1975) also indicated other differences between *H. depressum* and *H. orbiculare* in the grooves of the dorsal carapace surface and postocular lobes.

*H. depressum* is here restored to its original genus as a result of finding a species in Australia which shows affinities with *H. orbiculare* and *H. depressum*. *H. hodgkini* n.sp. is clearly a *Hymenosoma* species on the basis of having no epistome. However, it differs from *H. orbiculare* in a number of features and in some of these it is more like *H. depressum*. For example, *H. hodgkini* n.sp. shares with *H. depressum* an unusual modification of the female abdomen in which the abdomen is projected posteriorly at segment 3 into two lateral bulges (Fig. 2E). Table 1 gives a series of features in which the three species differ. Summarizing the data of this table, *H. orbiculare* and *H. hodgkini* n.sp. are most alike in eight features, *H. orbiculare* and *H. depressum* are most alike in seven features and *H. hodgkini* n.sp. and *H. depressum* are most alike in three features. *H. orbiculare* and *H. hodgkini* n.sp. are similar in more conservative features: epistome, carapace grooves and male 1st pleopod. Hence, in dividing these species into two groups, *H. depressum* would be the separated species. However, the three species are much more closely related to each other than to any other hymenosomatid species and the affinity warrants recognition as one genus. This has necessitated a modification of the diagnosis of the genus *Hymenosoma* Desmarest to encompass the three species.

Specimens of *H. orbiculare* have now been reported from localities in southern Africa ranging from the sublittoral, down to 80 m (Barnard, 1950), to estuaries, to a freshwater lake (Allanson et al., 1966; Boltt, 1969); a surprising distribution even for a euryhaline species. There are morphological differences between specimens from deep sublittoral habitats and inshore or estuarine habitats. The specimens from deeper water mature at a smaller size, are more granulose, their rostrum is trilobate, through development of the lateral portions above the eyestalks, and the rostrum projects upward and beyond the eyes in some specimens, e.g. Barnard (1955, Fig. 5). Not all specimens from deeper water are as extreme as the specimen figured by Barnard (1955): the specimens from 9-37 m in Simon's Bay examined in this study (see Material Examined) are intermediate between Barnard's specimen and the "inshore" *H. orbiculare*, but in these Simon's Bay specimens the rostrum is distinctly trilobed. Stimpson (1858) described a granulose specimen as *H. geometricum*, which was subsequently treated as a junior synonym by Stebbing (1914) on the grounds that it was within the variability of *H. orbiculare*. Later workers, e.g. Barnard (1950) and Broekhuysen (1955), have tentatively come to the same conclusion. The size differences at maturity may be phenotypic variation, but the other morphological variation is genetic. It is a greater degree of morphological variation than in any other hymenosomatid and this, with the great range of habitats, makes it quite possible that several species are represented.

MATERIAL EXAMINED: (other than Australian specimens) *Hymenosoma orbiculare*: Simon's Bay, Cape of Good Hope, South Africa, undated, 3 ov.♀♀, 5-20 faths, ex British Museum "Challenger" Collection, June 1897 (AM G.1641); Simon's Bay, South Africa, undated, ♂♂ and ♀♀, 5-20 faths, "Challenger" Collection (BM 84.31). *Hymenosoma depressum*: Blueskin Bay, near Pt. Chalmers, New Zealand, Dec. 1918, C. Hedley, ♂ (AM P.4432); Akaroa Heads, New Zealand, undated, 4♂♂, 2 im.♀♀, in eight faths, Suter

Collection (BM 99.7.18.15).

### **HYMENOSOMA HODGKINI** n.sp.

Figs. 2E, 6H, 7I, 10B, 10C

TYPE LOCALITY AND TYPES: Budgewoi Lake, Toukley via Wyong, N.S.W., Australia. HOLOTYPE: Mar. 1947, I. Bennett, ♂ (7.5 mm, 1st pleopod detached and mounted on slide), tow-netted (AM P.11723); PARATYPES: collection details as for Holotype, 10♂♂ (3.5-<7.5 mm, one male with 1st pleopod detached and mounted on slide), 4 ov. ♀♀ (5.7-7.2 mm), 2 im.♀♀(4.7, 5.4 mm) (AM P.11723); Lake Macquarie, N.S.W., Nov. 1894, M. Waite, ♂ (AM G.1210); Narrabeen Lakes, near Sydney, N.S.W., 12.i.1940, H. E. Smythe, im. ♀ (AM P.11260); The Gut, Brooklyn, Hawkesbury R., N.S.W., 6.ix.1975, ♂, ov. ♀, Transect A (through mangrove stand, *Avicennia marina*) Australian Littoral Society (AM); Moreton Bay, undated, ♂, 2 ov.♀♀, from sample 925 location 94A mud and from sample 448 location 35A mud (CSIRO).

DISTRIBUTION: Coastal marine lakes and Hawkesbury River, N.S.W., and Moreton Bay, Queensland, Australia.

DIAGNOSIS: Dorsal carapace surface with well defined grooves; rostrum much shorter than eyes, not reaching corneas; without an epistome; dactyli of walking legs with a row of fine teeth; mature female abdomen projecting posteriorly in two large bulges at segment 3.

DESCRIPTION: Carapace width to length ratio 0.92-1.07; dorsal carapace surface subcircular (Fig. 2E), with a distinct rim and groove around circumference, with gastro-cardiac, cervical and thoracic grooves well defined, other grooves weak; lateral carapace walls shallow, sloping out ventrally; rostrum deflexed with broad lateral processes over eyestalks; eyestalks elongate, largely visible dorsally; acute postocular lobes adjacent to eyestalks; antennules elongate, reaching far beyond eyes; without an epistome and consequently without an interantennular septum or antennal spines; rostral keel absent; subhepatic regions visible dorsally, with an obtuse tooth located behind postocular lobe, immediately beneath antero-lateral carapace rim; anterior of mouth-field marked by a small sunken ridge below antennules, antero-lateral margins of mouth-field developed into acute rounded prominences, conspicuous dorsally and projecting more anteriorly than rostrum; 3rd maxillipeds more than ¾ filling mouth-field, ischium subequal with merus along lateral edges; length of male chelipeds between 1.5-2 X carapace width, merus long, propodus inflated, fingers occupy ca.⅓ total propodus length, fingers gape proximally, dactylus with a long basal tooth in gape, fingers meet distally with fine serrations on cutting edges; length of female chelipeds less than 1½ X carapace width, with fine tubercles on anterior surfaces, fingers occupy ca. 0.4 of total propodus length, fingers not gaping, cutting edges with fine serrations; walking legs slender, length 2.5-3 X carapace width, dactyli elongate and slightly curved (Fig. 6H), tapering gradually to a point, ventral margin with a row of very fine teeth getting progressively longer distally, dense long setae on ventral edges of dactyli (not figured); female abdomen conspicuous dorsally (Fig. 2E), eggs visible through segment 3 of ovigerous females in dorsal view, with two submedial grooves extending from distally on segment 3 to telson, segments 5, 4 and telson progressively shorter, telson broad, arcuate, abdomen broadest at segment 5; female genital aperatures not covered by abdomen in large immature females (small immature females?); eggs ca. 0.3 mm diameter; male abdomen sculptured making segmentation difficult to distinguish (Fig. 7I), abdomen broadest at segment 1, segment 1 with a medial prominence, conspicuous in dorsal view, segment 2 short, almost concealed by segment 1 when abdomen straightened, segment 3 of similar breadth to segment 2, slightly longer than segment 1, with a small medial prominence, segment 4 narrower and shorter than segment 3, segment 5 elongate narrow, constricting to narrowest point of abdomen then expanding slightly, telson trapezoidal, with rounded angles distally, with small intercalated plates laterally; distal portion of male 1st pleopod relatively straight (Fig. 10C), with a row of long setae on sternal side, apex partially rimmed with curved setae and with a dense zone of denticles on abdominal side (Fig. 10B); colour pale (preserved specimens); sparse long setae on walking legs, dense setation on mouthparts around Milne Edwards apertures and on dactyli of walking legs; males up to 7.5 mm, mature females 5.7-7.2 mm.

REMARKS: In *H. orbiculare* and *H. hodgkini* the most anterior structures, excluding the eyes, are acute lobes situated ventral to the eyes. These lobes are called exterior orbital angles by Stimpson (1907), Tesch (1918) and Barnard (1950). I consider that they are projections of the antero-lateral angles of the mouth-frame, rather than parts of the orbits. These angles of the mouth-frame are prominent in the other species, *H. depressum*, but not visible in dorsal view; and in the two species without epistomes the angles are considered to have become very prominent. This may be an academic point, since, in the absence of an epistome, the mouth-frame is continuous with the subhepatic region bordering the eyestalks. However, these acute lobes should not be confused with postocular lobes in *H. orbiculare*, as in Gordon (1966). *H. hodgkini* has acute postocular lobes in the normal position as well as the prominences ventral to the eyes. *H. orbiculare* does not have normal postocular lobes; there is an acute tooth on the subhepatic region somewhat lateral to the eyestalks and this may be homologous to the acute postocular lobes of *H. hodgkini* and *H. depressum*.

*H. hodgkini* has intercalated plates between segment 5 and the telson of the male abdomen, a unique feature which is also shown by the *Amarinus* n.gen. species. Among Brachyura it is only known from one other family, Dromiidae (Holthuis, 1968). Intercalated plates are not present in *H. orbiculare* or *H. depressum*.

*H. hodgkini* has been collected from five localities in a section of the eastern Australian coast between Sydney and Brisbane. At these localities marine salinities prevail, but salinity is lowered during summer months by freshwater discharge.

*H. hodgkini* is named in honour of Dr E. P. Hodgkin, who, as Reader in Zoology, University of Western Australia, supervised my Ph.D. studies on hymenosomatids.

MATERIAL EXAMINED: Type specimens listed above.

## **ELAMENA** H. Milne Edwards, 1837

*Elamena* H. Milne Edwards, 1837: 33-4 (type species, by monotypy, *Hymenosoma mathaei* Desmarest, 1825).

DIAGNOSIS: Carapace, with rostrum, polygonal to pear-shaped; dorsal carapace surface without well defined grooves except for a gastro-cardiac groove present in some species; rostrum truncated or triangular, continuous with carapace surface, concealing antennae, antennules and most of eyes; rostral keel deep, forming a distinct T-shape with rostrum rim anteriorly (all species with truncated rostra and three with triangular rostra), rostral keel poorly developed, or absent; epistome long, usually almost as long as broad; pterygostomial regions often with one or two prominent lobules; 3rd maxillipeds broad, almost completely filling the mouth-field, ischium subequal to or longer than merus along lateral edge; chelipeds stouter than walking legs, particularly in large males; length of walking legs 1½-3 X carapace width, dactyli usually with two subterminal teeth; female abdomen circular to ovate, without fused segments except in two very small species, terminal edge of telson often concave; male abdomen without fused segments (two species) or with segments 3-4 (or 3-5?) fused; male 1st pleopods strongly curved and twisted above a stout base, usually bearing large subterminal setae.

SPECIES OF *ELAMENA:* Based on Kemp (1917), Chopra and Das (1930), Gordon (1940), Monod (1956), and Melrose (1975).

| **Species** | **Distribution** |
|---|---|
| **E. mathaei* (Desmarest, 1825) | Red Sea; S.E. Africa; Mauritius |
| **E. truncata* (Stimpson, 1858) | Indo-West Pacific |
| **E. producta* Kirk, 1879 | New Zealand |
| *E. longirostris* Filhol, 1885a | New Zealand |
| *E. sindensis* Alcock, 1900 | India; Sri Lanka |
| *E. gracilis* Borradaile, 1903 | Maldive Archipelago |
| *E. cimex* Kemp, 1915 | Chilka Lake, India; Madagascar |
| *E. xavieri* Kemp, 1917 | Mandavi R., India |
| **E. cristatipes* Gravely, 1927 | India |
| **E. abrolhensis* Gordon, 1940 | southern Australia |
| *E. gordonae* Monod, 1956 | W. Africa; N.E. Australia |
| **E. momona* Melrose, 1975 | New Zealand |
| *E. umerata* n.sp. | northern Australia |

REMARKS: The *Elamena* species can be grouped according to the shapes of their rostra into "truncated" species (indicated with an asterisk in the preceding list) and "triangular" species, with *E. cristatipes* being closest to an intermediate condition. Species in the two groups tend to differ in body form (polygonal versus pear-shaped), development of the rostral keel and armature of the pterygostomial region, but the differences are inconsistent and no separate taxonomic status for these groups is proposed. The "triangular" species resemble the *Trigonoplax* species and have been included within this taxon by authors who treated *Trigonoplax* as a subgenus of *Elamena*. In this study *Trigonoplax* is recognised as a genus with three distinctive species which are clearly distinguished from "triangular" *Elamena* species (see Remarks on the genus *Trigonoplax*).

Some authors, e.g. Kemp (1917), consider that fusion of male abdominal segments is a diagnostic character of the genus *Elamena*. However, in two New Zealand species described by Melrose (1975) there is no fusion. Chopra and Das (1930) and Gordon (1940) together describe six *Elamena* species in which they consider that segments 3-4 are fused; Kemp (1917) and Barnard (1950) together describe five species (three in common with the previous authors) in which they consider that segments 3-5 are fused. This discrepancy probably arises from different interpretations of five articulated portions present in the male abdomen and telson of all these species. Depending on whether the author considered that there were normally six or seven segments present, two or three segments respectively were considered to be fused and the sutures obliterated. Hymenosomatids have five abdominal segments plus the telson (see Remarks, page 9) and it is likely that only two medial segments are fused in the male abdomen of *Elamena* species.

Zoeae are known for a surprising number of *Elamena* species: five "truncate" species and two "triangular" species (page 153). Their expanded abdomens are a distinctive character, only known in some zoeae of two other brachyuran families, Pinnotheridae and Ocypodidae (Wear, 1968); and, with the exception of *Neohymenicus pubescens,* only present in *Elamena* species within the family Hymenosomatidae. *H. pubescens* zoeae differ from *Elamena* zoeae in having dorsal and lateral carapace spines. Larval morphology supports the *Elamena* taxon presented here.

## **ELAMENA TRUNCATA** (Stimpson)

Figs. 2D, 6D, 8B, 10H

*Trigonoplax truncata* Stimpson, 1858:109; 1907:146-7.

*Elamene truncata* A. Milne Edwards, 1873:323.— Henderson, 1893:395.

*Elamena truncata.* —Kemp, 1917:272-4, figs. 22, 23. —Sakai, 1932:44, fig. 2; 1938:201, pl. 20 fig. 3; 1976:152-3, pl. 47 fig. 2.— Gordon, 1940:67-8, fig. 5.— McNeill, 1968:47.

[?] *Elamena truncata.* —Tesch 1918:22-24, pl. 1 figs. 4, 4a-c (confused with several *Elamena* species).

[not] *Elamena truncata.* (=*E. abrolhensis*) —Baker, 1906:112-3, pl. 2 figs. 2, 2a-c. —Hale, 1927:119-20, fig. 117. — Montgomery, 1931:426-7, pl. 27 fig. 2.

TYPE LOCALITY AND TYPES: Amami Ohsima and Loo Choo, Japan. No type specimens are extant. They were probably lost in the 1871 Chicago fire with nearly all of the invertebrate collections of the North Pacific Exploring Expedition (see Introduction of Stimpson (1907) and Garth (1958)). None of Stimpson's hymenosomatid types is in the Smithsonian Institution (F. A. Chace, pers. comm.) nor in Peabody Museum of Natural History (W. D. Hartman, pers. comm.), other possible locations of Stimpson's types suggested by Evans (1967).

DISTRIBUTION: Japan, India, Indonesia (?), New Caledonia, and N.E. Australia.

DIAGNOSIS: Carapace width greater than length; posterior lateral angles of carapace rounded and not evident; dorsal carapace surface usually without ridges extending in from angles; rostrum truncated; rostral keel deep, discontinuous with interantennular septum; terminal spine on carpus of walking legs subequal with terminal spine on merus of walking legs; male 1st pleopods bent at ca. 90°, with four or five subterminal setae.

DESCRIPTION: The following are additions to the descriptions of *E. truncata* by Kemp (1917), Sakai (1938) and Gordon (1940) and the Diagnosis:— carapace width to length ratio 1.06-1.22 (Fig. 2D); dorsal carapace surface slightly concave or convex, a faint gastro-cardiac groove sometimes present; rostral keel deep, triangular in lateral view; 3rd maxillipeds often with a well-defined longitudinal ridge on merus, extending to ischium; largest male 6.2 mm, mature females 5.6-9.3 mm.

REMARKS: This species has the greatest reported distribution of the *Elamena* species, being reported from widely separated localities in the Indo-West Pacific region. However, reports of *E. truncata* from Zanzibar, Sri Lanka and southern Australia are considered erroneous and they are referred to *E. mathaei*, *E. sindensis* and *E. abrolhensis,* respectively (Gordon, 1940). The specimens of *E. truncata* described by Tesch (1918) are unusual. A female figured (Tesch, pl. 1 fig. 4b) is like *E. abrolhensis,* but the posterior lateral carapace angles are even more pronounced and pointed, while a male figured (Tesch, pl. 1 fig. 4) is more like a typical *E. truncata.* In Tesch's general description of the specimens, he gives three features which differ from both *E. truncata* and *E. abrolhensis:* three lobules in the pterygostomial regions, exopodites of the 3rd maxillipeds well exposed, and penultimate segment (5) of the male abdomen shorter than the two preceding segments (3 and 4, or 2 and fused 3-4?) and the telson.

The type specimens of *E. truncata* are not extant and it was not possible to obtain Japanese specimens with which to compare the Australian material. However, Sakai (1932, 1938) figures and describes Japanese specimens and by comparison with Sakai's descriptions, and following Gordon (1940) and McNeill(1968), *Elamena* specimens from northern Australia are attributed to *E. truncata.*

MATERIAL EXAMINED: Lifton, Loyalty Islands, Aug. 1925, A. F. Bassett Hull,♂, 2 ov.♀♀ (AM P.8279). New Caledonia, 1926, A. F. Bassett Hull, ov.♀ (AM P.8889). QUEENSLAND: Port Denison, 1918, ♂, ov.♀, 2 im.♀♀ (AM P.4232); Holbourne Island, Nov. 1921, E. H. Rainford, im. ♀(AM P.5555); High Island Reef, 15.vii.1924, W. E. J. Paradice,♂(AM P.8024); High Island Reef, 1924, W. E. J. Paradice, ov.♀ (distorted) (AM P.7975); Flinders Island, Princess Charlotte Bay, Sept. 1930, W. L. Wassell,♀(AM P.10105); Low Isles, 15.viii.1963, J. Bryan, im. ♀on reef flats (AM P.16585); Low Isles, 27.vi.1973, J. S. Garth, 2♂♂, im.♀, on reef flat under coral rubble (AHF JG-22-73).

### **ELAMENA ABROLHENSIS** Gordon

Figs. 2A, 6C, 8G, 10I

*Elamena truncata.* —Baker, 1906: 112-3, pl. 2 figs. 2, 2a-c. —Hale, 1927: 119-20, fig. 117.—Montgomery, 1931: 426-7, pl. 27 fig. 2.

*Elamena abrolhensis* Gordon, 1940: 70-1, figs. 6b, c, 7a-c, 10a.

TYPE LOCALITY AND TYPE: Sandy Island, Abrolhos Islands, Western Australia; HOLOTYPE:♂ (6.6 mm) (BM 1931.7.24.37).

DISTRIBUTION: South Western Australia and South Australia, as far north as the Abrolhos Islands on the west coast.

DIAGNOSIS: Carapace width greater than length; posterior lateral angles of carapace pointed and obtuse; carapace dorsal surface usually with ridges extending in from angles; rostrum truncated; rostral keel deep and long, continuous with prominent interantennular septum; postocular lobes with small acute spines; terminal spine on carpus much shorter than terminal spine on merus of walking legs; male 1st pleopods S-shaped, with ca. 12 subterminal setae.

DESCRIPTION: The following are additions to the description of *E. abrolhensis* by Gordon (1940): — carapace width to length ratio 1.04-1.18, greatest in large specimens (Fig. 2A); anterior lateral angles not usually as pronounced as in Gordon's fig. 6b; dorsal carapace surface slightly concave or convex, rimmed, often with a gastro-cardiac groove and a median longitudinal ridge; rostrum obscuring all but tips of eyes dorsally; no antennal spines; epistome width to length ratio ca. 1.5; 3rd maxillipeds almost completely enclosing mouth-field, ischium subequal with merus along lateral edge, segment 3 of palp much longer than segments 1 and 2; walking legs ca. 2 X carapace width; chelipeds of large males larger than similar sized females and with a basal tooth on dactylus; telson truncated, longest segment of female abdomen; setation limited to mouthparts, Milne Edwards apertures, dactyli of walking legs, and edge of female abdomen; colour yellow, yellow-green, red-brown, not mottled; largest male 7.7 mm, mature females 6.8-8.4 mm.

MATERIAL EXAMINED: SOUTH AUSTRALIA: Parkside, 22.v.1906, W. H. Baker, ♀, Fulton Collection (NMV); Moonta, Feb. 1937, K. Reed, ♂ (AM P.10838); South Australian coast, undated, 2 ov.♀♀ (dried specimens), labelled *Elamena truncata* (SAM). WESTERN AUSTRALIA: Lucky Bay, east of Esperance, 4.xii.1921, Hull, Grant and Wright, ♂, im.♀ (AM P.5684, P.5679); Hopetown, 9.i.1959, R. W. George, ov.♀, from granite rocks at low tide (WAM); Yanchep, 27.i.1959, R. W. George, ♂, on reef flat (WAM); Cottesloe, near Green Island, 3.x.1960, M. Tyndale-Biscoe, ♂ (WAM); Pt. Peron, 8.ix.1962, W. H. Butler, im.♀ (WAM); Horricks Beach, 11.xii.1964, J.S. Lucas, ♂ (1st pleopod mounted on slide), ♀, under rocks in littoral area of reef (AM P.20169); Radar Reef, Rottnest Island, 13.xii.1964, J.S. Lucas, im.♀, among corals and ascidians on undercut of reef flat (WAM); Armstrong Pt., Rottnest Island, 5.i.1965, B. F. Phillips, ♀, under rock on intertidal platform, ovigerous when collected, larvae from eggs developed in the laboratory (WAM).

### **ELAMENA GORDONAE** Monod

Figs. 2B, 6E

*Elamena (Trigonoplax) gordonae* Monod, 1956: 469-72, figs. 629-637.

TYPE LOCALITY AND TYPES: West Africa, between Conakry and Monrovia. HOLOTYPE: undated, ov.♀ (2.8 mm) 30-40 m, Debyser collection (MHN); PARATYPE: Sierra Leone coast, 1948, ♀ (3.0 mm, without abdomen) collected by "Maid Honour" (MHN). The specimens were recently examined by Dr. J. Forest (pers. comm.).

DISTRIBUTION: Western Africa and N.E. Australia.

DIAGNOSIS: Dorsal carapace surface convex, sloping up to a medial longitudinal ridge for most of carapace length; rostrum triangular, without keel or spine on ventral surface; postocular lobes undeveloped; one prominent lobe in pterygostominal region; dactyli of walking legs with two subterminal teeth; female abdomen broader than carapace width, conspicuous at posterior of carapace in dorsal view; female pleopods project laterally from abdomen; mature females less than 3 mm carapace width.

DESCRIPTION: The following is additional to the description of Monod (1956) and the Diagnosis. The descriptions are based on four female specimens, no male specimens having been examined:— carapace width to length ratio 0.85-1.00; dorsal carapace surface with a faint gastro-cardiac groove (Australian specimens); lateral carapace wall vertical; rostrum outreaching eyes but not antennules; no antennal spines; ischium of 3rd maxillipeds subequal with merus along lateral edge; cheliped length 1½ X carapace width; female abdomen large compared to body size, segments 1-4 visible dorsally at posterior, segments 1 and 2 short, segments 3, 4, 5 and telson progressively longer, widest at segment 5, possibly some segments fused with sutures remaining; eggs 0.35 mm diameter.

REMARKS: Monod's figures do not show the size of the female abdomen (Monod, 1956): the abdomen is omitted in Fig. 629 and only the small segments 1 and 2 are shown in Fig. 630. Dr. J. Forest (pers. comm.) examined the type specimens and advised that the abdomen of the holotype is as in the Australian specimens; the abdomen is missing in the paratype. See the Remarks on *Halicarcinus hondai* for discussion of female abdomens.

There are only small differences between the west African and Australian specimens: the rostrum has a more rounded apex in the Australian specimens and a faint gastro-cardiac groove is present. Monod (1956) described a "ligne carénée médian gastro-cardiaque", which is perhaps the groove in his specimens, although it isn't figured. Even the faint ridges on the dorsal carapace surface, described by Monod, are present in the Australian specimens and it is considered that they are conspecific. The two regions where *E. gordonae* has been collected are in the tropics, but they are widely separated, i.e. eastern Atlantic versus western Pacific. Also remarkable is that three species to which *E. gordonae* is closely related are Indian species, *E. sindensis, E. cimex* and *E. xavieri,* two of which occur in low salinity habitats.

*E. gordonae* is smaller than the other "triangular" *Elamena* species, except *E. umerata* n.sp., and it is the only *Elamena* species with an expanded female abdomen. A combination of other features included in the Diagnosis also distinguishes it from the other "triangular" species.

MATERIAL EXAMINED: Queensland: Tyroom Rds, Gt. Sandy Strait, Mar. 1952, J. S. Hynd, 2 ov.♀♀, 10 faths (AM P.12208).

## **ELAMENA UMERATA** n.sp.

Figs 2C, 6F, 9B

TYPE LOCALITY AND TYPES: Darwin, Northern Territory, Australia. HOLOTYPE: Dec. 1923, W. E. J. Paradice,♀ (2.8 mm; only four legs and one cheliped, all detached, are present), from among marine growths on piles of Rail Pier (AM P.6819); PARATYPE: Tyroom Roads, Great Sandy Strait, Queensland, 6.vi.1946, J. S. Hynd,♂(ca. 2.1 mm, the specimen is distorted through drying out at some stage), 10 faths, *Zygometra microdiscus* and spiny alcyonarian also in catch (AM P.12217).

DISTRIBUTION: Northern Australia (two known localities).

DIAGNOSIS: Dorsal carapace surface concave, with lateral carapace margins upturned; anterior lateral carapace angles very prominent, rounded and slightly obtuse; antero-lateral carapace borders at right angles to longitudinal body axis; rostrum equilateral triangular with rounded apex, without keel or spine ventrally; female abdomen with segments 3-5 fused and no sutures evident; male 1st pleopod with thin distal portion curving through two-thirds of a circle, without subterminal setae.

DESCRIPTION: Carapace width to length ratio 0.88 (♀) (Fig. 2C); a faint gastro-cardiac groove present on dorsal carapace; lateral carapace walls sloping slightly out ventrally; posterior lateral angles obtuse and rounded; rostrum laterally concave, pointing slightly upwards, almost concealing eyes and antennules; eyestalks very short; postocular lobes undeveloped; interantennal septum a strong ridge; antennal spines absent; epistome length subequal with breadth; pterygostomial regions with two prominent lobes, one near mouth-field and one near base of cheliped, a further prominent lobe in subhepatic region; ischium of 3rd maxillipeds subequal with merus along lateral edge; male and female chelipeds ca. 2 X and 1.5 X carapace width, respectively, stouter than walking legs, propodus more inflated in male than female, fingers of chelae strongly curved distally; fingers of female chelae without gapes and with fine teeth on cutting edges; fingers of male chelae meet distally, dactylus with two large basal teeth and four teeth distally, propodus finger with one basal tooth, which fits between large teeth on dactylus, and a row of teeth distally; legs moderately slender, longer than 2 X carapace width, a prominent terminal spine on merus, dactylus tapering, strongly curved distally, with two large recurved teeth subterminally (Fig. 6F); a row of setae on ventral surface of dactylus increasing in length distally; female abdomen not broader than carapace width, only segments 1 and 2 visible dorsally, segments 1 and 2 short, telson trapezoidal, ca. ⅓ total length of abdomen, segments 1 and 2 of similar width, abdomen increasing in breadth progressively from segment 3 to junction of segment 5 and telson, pleopods project laterally from abdomen; male abdomen with segments 3 and 4 fused and no suture evident, segments 1 and 2 very short, segments 3-4 longest section of abdomen, segment 5 shorter than telson, telson spade-shaped, segments 1 and 2 of similar width, abdomen expands to maximum width mid-way along segments 3-4 and then narrows to segment 5, segment 5 narrows further towards junction with telson (distorted abdomen, not figured); male 1st pleopod with stout base and thin distal portion strongly curved and twisted, tapering terminally to a long point (Fig. 9B); little setation except for dactyli of walking legs and short setae on lateral borders of rostrum; mature female less than 3 mm carapace width.

REMARKS: *E. umerata* differs from the other "triangular" *Elamena* species in having very pronounced anterior lateral angles. This condition is opposed to the usual "triangular" body form which tends to a triangular or pear-shaped form, with anterior lateral angles very obtuse and rounded and little evident. *E. umerata* also has unusual features of the male and female reproductive morphology. The male 1st pleopod is more uniformly curved than in other *Elamena* species which have been described, so that the thin distal portion curves through two-thirds of a circle. In other *Elamena* species, the male 1st pleopod bends through ca. 90° and then is either relatively straight distally or it bends again to make an approximately S-shape. Also, it is the only species with no subterminal setae on the male 1st pleopod; so that the pleopods are more like those of some *Halicarcinus* species than *Elamena* species. Fusion of segments in the female abdomen is possibly shown by *E. gordonae,* but in *E. umerata* the condition is further advanced because no sutures remain between the fused segments. The abdomen is not expanded as in *E. gordonae*. For further discussion of the abdomens of small females see the Remarks on *Halicarcinus hondai.*

*E. umerata* is related to the "triangular" *Elamena* species and is most similar to the other very small species, *E. gordonae*. These two species have been collected at the same locality off the Queensland coast.

The name *umerata* (shoulder-possessing; Latin, feminine) refers to the prominent anterior lateral angles of the carapace, giving the appearance of "shoulders".

MATERIAL EXAMINED: Type specimens listed above.

## **HALICARCINUS** White, 1846

*Halicarcinus* White, 1846:178 (type species, by original designation, *Cancer planatus* Fabricius, 1775).

*Liriopea* Nicolet, 1849:158 (type species, by subsequent designation of Rathbun (1925), *Hymenosoma leachi* Guérin, 1838 = [?] *Cancer planatus* Fabricius, 1775).

*Hymenicus* Dana, 1851:253 (type species, by subsequent designation of Kemp (1917), *Hymenicus varius* Dana, 1851).

*Hombronia* Lucas, 1853:60 (type species, by monotypy, *Hymenosoma ? tridentatum* Jacquinot, 1853 = [?] *Cancer planatus* Fabricius, 1775).

*Rhynchoplax* Stimpson, 1858:109 (type species, by subsequent designation of Kemp (1917), *Rhynchoplax messor* Stimpson, 1858).

DIAGNOSIS: Carapace subcircular or suboval, laterally or longitudinally elongate; dorsal carapace surface with at least gastro-cardiac, cervical and thoracic grooves well defined; often with an acute spine at either posterior or anterior lateral carapace angles; rostrum separated from dorsal carapace by a ridge or groove or both; rostrum basically trilobate, but varying markedly in degree of fusion of lobes and relative lengths of medial and lateral lobes; epistome short and broad, breadth usually at least 2 X length; pterygostomial regions usually with lobules or spines; 3rd maxillipeds broad, almost completely filling mouth-field; ischium subequal with or shorter than merus along lateral edge; chelipeds stouter than walking legs, especially in large males; walking legs slender to stout, dactyli usually with one or two rows of small teeth and often with one or two large teeth subterminally; female abdomen usually without fused segments; male abdomen without fused segments, except in *H. hondai*; male 1st pleopods either with distal portion thin, strongly curved toward abdomen and with very short setae, or distal portion thin to moderately stout, little curved and with long setae.

SPECIES of *HALICARCINUS:* Based on Sakai (1938), Lucas (1968), Takeda and Miyake (1971b), Melrose (1975) and Takeda and Nunomura (1976).

| **Species** | **Distribution** |
|---|---|
| *H. planatus* (Fabricius, 1775) | circum-subantarctic |
| *H. varius* (Dana, 1851) | New Zealand |
| *H. ovatus* Stimpson, 1858 | southern Australia |
| **H. messor* (Stimpson, 1858) | Japan |
| **H. setirostris* (Stimpson, 1858) | Japan; China |
| *H. minutus* (A. Milne Edwards, 1873) | New Caledonia |
| *H. whitei* (Miers, 1876) | New Zealand |
| *H. rostratus* (Haswell, 1882a) | southern Australia |
| *H. cookii* (Filhol, 1885b) | New Zealand |
| **H. coralicola* (Rathbun, 1909) | Japan; Taiwan; Singapore |
| *H. bedfordi* Montgomery, 1931 | northern Australia |
| *H. orientalis* Sakai, 1932 | Japan |
| *H. innominatus* Richardson, 1949b | New Zealand; Tasmania |
| **H. keijibabai* (Takeda and Miyake, 1971b) | New Caledonia |
| **H. hondai* (Takeda and Miyake, 1971b) | Ryukyu Is.; Gt Barrier Reef |
| *H. tongi* Melrose, 1975 | New Zealand |
| *H. afecundus* n.sp. | northern Australia |

REMARKS: The three species attributed to *Rhynchoplax* Stimpson (1858) by Sakai (1938, 1965) and two further *Rhynchoplax* species described by Takeda and Miyake (1971b) are congeneric with the *Halicarcinus* species. (The five species are marked with an asterisk above.) Sakai (1938) made a review of the confused literature on *Rhynchoplax*, giving a diagnosis of the genus and separating most of the species previously included in *Rhynchoplax* into a new genus, *Neorhynchoplax* Sakai (= *Elamenopsis* A. Milne Edwards, see page 191). Sakai recognised that the *Rhynchoplax* (s.s.) species closely resemble the *Halicarcinus* species and the characters by which he appeared to distinguish them were: *Rhynchoplax* species have a long medial rostral lobe, while *Halicarcinus* species have subequal lobes, and *Rhynchoplax* species have less stout male chelipeds. Stimpson (1858, 1907) also gave long medial rostral lobe as a generic character of *Rhynchoplax*; while most of the other characters that he gave in his diagnosis are applicable to at least some *Halicarcinus* species.

The species included in *Halicarcinus* and *Rhynchoplax* may be ordered according to the relative lengths of the medial and lateral rostral lobes. The series from lateral lobes relatively longest to medial lobe relatively longest is: *afecundus* n.sp., *planatus, tongi, innominatus, cookii, ovatus, orientalis, minutus, varius, whitei, bedfordi, coralicola*, keijibabai*, setirostris*, messor*, rostratus, hondai**. The species towards the end of the series have rostral lobes more fused than those towards the beginning of the series, they also tend to be smaller, more spiny and more slender-legged than those earlier in the series. However, these are only tendencies and there is no basis in these characters for a division into two taxa, e.g. *H. hondai*, the species with relatively longest medial rostral lobe, is also the smallest species, but it has stout legs. Two distinct forms of 1st male pleopod occur among these species: one with a strongly curved, distal portion, e.g. Fig. 9C, and the other which is little curved, e.g. Fig. 9E. The former pleopod occurs in the species from *planatus* to *whitei* in the above series, and in *setirostris, messor* (Fig. 9A) and *hondai*; the latter occurs in *bedfordi, coralicola* and *rostratus*. (*afecundus* n.sp., *minutus* and *keijibabai* are yet to be described.) This is another character showing a tendency, but no clear division, between species early and late in the series. The difference in 1st male pleopods is the most important difference among these species. However, it is not proposed to remove *H. bedfordi, H. coralicola* and *H. rostratus* as they belong in this taxon in all other respects.

There are two hymenosomatid species which may belong in the genus *Halicarcinus* although their trilobate rostra are figured by authors as being continuous with the dorsal carapace surface. Neither of these species has been reported since the original description. The species are:—

1. *Hymenicus krefftii* Hess, 1865, type locality Sydney, Australia. The type specimens were destroyed in the Zoological Museum, Göttingen, Germany, during World War II (P. Kuenzer, pers. comm.). No specimens identified as *H. krefftii* are present in Australian museum collections and no specimens corresponding to Hess' brief description were collected by Lucas (1968). de Man (1887a), examining one of the syntypes, corrected Hess' description and concluded that the specimen appeared to be the same as *Halicarcinus cookii*, a New Zealand species. Sakai (1938) included it in his list of *Neorhynchoplax* species, with a question mark, but there is no evidence that Sakai examined specimens and Hess' description does not include the diagnostic features of *Neorhynchoplax* Sakai. If the type locality is correct, then Hess' specimens were probably *Halicarcinus ovatus*, which he badly described. Since the types are lost and the description is inadequate, the identity of *H. krefftii* remains unresolved.

2. *Elamene filholi* de Man, 1887b, type locality Noordwachter Island, near Djakarta, Java. This is an unusual species in that the eyes are situated well behind the anterior rim of the carapace and thoroughly concealed in dorsal view. The condition is like *Halicarcinides nuytsi*. de Man's description is fairly comprehensive and some important features which he omits are shown in his figures. Fig. 3 clearly shows the rostral lobes continuous with the dorsal carapace surface and Fig. 3a shows broad 3rd maxillipeds, almost meeting medially, with ischium and merus subequal in length. The maxilliped condition precludes inclusion of *Elamene filholi* in *Neorhynchoplax*, as proposed by Sakai (1938). The type specimens were not located.

MATERIAL EXAMINED: (other than Australian localities) *Halicarcinus messor*: Simoda, Japan, Apr. 1934, T. Sakai, ♂ ♂ (one 1st pleopod removed and mounted) and ♀ ♀, labelled *Rhynchoplax messor* (AM P.10497).

### **HALICARCINUS OVATUS** Stimpson

Figs. 3B-E, 6J, 6K, 7E, 9C

*Halicarcinus ovatus* Stimpson, 1853:109. — Lucas, 1971:475-82, figs. 3I, 4 (larval morphology). — Griffin and Yaldwyn, 1971:45-6. — Griffin, 1972:65. — Melrose, 1975:39-44, figs. 14-15.

For other Synonymy see Melrose (1975).

TYPE LOCALITY AND TYPES: Port Jackson, Australia. No type specimens are extant (see comments on type specimens of *Elamena truncata).*

DISTRIBUTION: Southern Australia, including Tasmania; from Geraldton on the west coast to Port Stephens on the east coast.

DIAGNOSIS: Rostrum arising from level with to distinctly below dorsal carapace surface, rostrum clearly trilobate, medial lobe slightly longer than lateral lobes, rostral lobes projecting forward in same plane, never deflexed, uniting at their bases beneath or slightly anterior to carapace rim; anterior lateral carapace angles obtuse; posterior lateral angles rounded obtuse, with a small acute spine; dactyli of walking legs with two irregular and closely approximated rows of teeth.

DESCRIPTION: Melrose (1975) gave a full description of *H. ovatus* specimens from two Australian localities; but she did not describe the variability of *H. ovatus* due to her limited material. Specimens of *H. ovatus* from different localities, and different habitats at the same locality, show considerable variation in the length and level of the rostrum, shape of the rostral lobes, general setation, fingers of male chelipeds, stoutness of walking legs and size of teeth on the dactyli of the walking legs (Lucas, 1968; Griffin and Yaldwyn, 1971; Griffin, 1972). Some of the variability is shown in Figs. 3B-3E and Figs. 6J and 6K. *H. ovatus* is the most ubiquitous of the Australian marine hymenosomatids, occurring on a range of substrates in the sublittoral, and this may account for the variability. Specimens from hard substrates subject to turbulence tend to have short rostra, arising below the carapace rim, stout legs and little body setation. These specimens resemble *H. planatus* and *H. innominatus,* which also live in this type of habitat. Specimens from soft substrates away from turbulence tend to have long rostra, arising from level with the carapace rim, moderate legs and considerable body setation. Intermediate conditions occur and no discrete divisions could be made on the basis of crab morphology although much material was examined. (*H. ovatus* is well represented in the Australian museum collections.)

Very variable coloration, white, yellow, orange, brown, red, black, often mottled or with patches of colour; females tending more to mottling and inconspicuous coloration; large males rarely exceed 10 mm, mature females 3.7-10 mm, mostly 5-6 mm.

REMARKS: In contrast to apparently continuous variation in crab morphology, three quite different kinds of larvae were produced by ovigerous females collected from different localities in S.W. Australia (Lucas, 1971). One of the larval morphs has distinctive features which it shares with zoeae of *H. planatus* (described by Boschi et al., 1969). On the basis of larval morphology, it is likely that the taxon being considered here is more than one species. It requires a morphometric study of crab morphology and correlation of crab and larval morphology for a range of females to clarify the situation.

*H. ovatus* has been reported from New Zealand, e.g. Balss (1930), and Melrose (1975) establishes that these reports are erroneous. She provides bases for distinguishing *H. ovatus* from the species in New Zealand and nearby, *H. varius, H. cookii, H. innominatus* and *H. planatus*, with which it has been confused.

MATERIAL EXAMINED: NEW SOUTH WALES: Port Stephens; Port Jackson; Long Reef, Collaroy; Shellharbour; Port Hacking; Jervis Bay; 32♂♂, 21 ov.♀♀, ♀, 2 im.♀♀ (AM P.94, AM P.95, AM P.7405, AM P.20178, AM P.20179). VICTORIA: Shoreham; Port Albert; Phillip I.; Rhyll; Flinders; Port Phillip; Beaumaris, Port Phillip; Lorne; Apollo Bay; 25♂♂, 11 ov.♀♀, 4♀♀, 3 im.♀♀, 7 juvs. (NMV 7 lots, AM P. 7486, AM P.11426). TASMANIA: Roches Beach, Frederick Henry Bay; Derwent Channel; D'Entrecasteaux Channel; Pt. Puer, Tasman Peninsula; 13♂♂, ov.♀, 4♀♀, 6 im.♀♀ (TM 14496/G212, TM 15061/G301, TM 19015/G652, TM G1052). SOUTH AUSTRALIA: Robe; The Bluff, Victor Harbour; Port Willunga; Streaky Bay; 11♂♂, 2 im.♀♀, 11 juvs. (SAM C19744, SAM C19745, NMV 1 lot). WESTERN AUSTRALIA: Horricks Beach, Geraldton; Rottnest I., Trigg I.; Blackwell Reach, Swan River; Woodmans Pt.; Cockburn Sound; various localities, Garden I.; Pt. Peron; Oyster Harbour; Dunsborough; Denmark; 24♂♂, 19 ov.♀♀, 4♀♀, 6 im.♀♀, 3 juvs. (WAM 11 lots).

## **HALICARCINUS ROSTRATUS** (Haswell)

Figs. 3F, 6L, 7F, 10H

*Hymenosoma rostratum* Haswell, 1882a:550; 1882c:116. — Baker, 1906:114, pl. 3 figs. 2, 2a,b.
*Halicarcinus rostratus*. — Kemp, 1917:247. — Hale, 1927:117-8, fig. 114. — Griffin and Yaldwyn, 1971:46. — Griffin, 1972:65. — Lucas, 1972:475-82, figs. 3H, 5A-5D (larval morphology).
*Rhynchoplax rostrata*. — Tesch, 1918:17, 18.
*Neorhynchoplax rostrata*. — Takeda and Miyake, 1971a:4.

TYPE LOCALITY AND TYPES: Griffith's Point, Port Western, Victoria, Australia. There are three specimens in the Australian Museum which, although not labelled as such, are undoubtedly syntypes. They are preserved in the same distinctive manner as the syntypes of *Hymenosoma australe* Haswell. Their details are: Griffith's Point, Victoria, undated, 2 ♂ ♂ (4.9 mm, 5.0 mm; both dried specimens, latter one in poor condition), Haswell Collection No. 213 (the specimens are glued to a glass plate with a red spot and a label cut from Haswell, 1882c) (AM P.15396), ♀ (4.2 mm, dried), Haswell Collection No. 213 (the specimen is glued to another glass plate with a label cut from Haswell, 1882c) (AM P.15397). The smaller male specimen, which is in better condition, is hereby designated lectotype of *Hymenosoma rostratum* Haswell.

DISTRIBUTION: Southern Australia including Tasmania; from Swan River on the S.W. coast to Montague I. on the S.E. coast.

DIAGNOSIS: Rostrum arising from level of dorsal carapace, lateral rostral lobes short, fused with medial lobe and little indicated, medial rostral lobe long and tapering, well outreaching eyes, without long hairs arising from apex; postocular lobes developed into acute teeth, conspicuous dorsally; posterior lateral carapace angles with an acute spine projecting dorsally, especially prominent in large males; three acute spines in pterygostomial regions; male 1st pleopods little curved, stout at base and tapering to a rounded tip, with rows of long setae on distal half.

DESCRIPTION: The following is additional to the descriptions of Haswell (1882a and c) and Baker (1906), which do not include details of females: — females not as spiny as large males, with shorter medial rostral lobe, spines at posterior lateral angles and pterygostomial spines than in large males; female chelipeds shorter than in large males (ca. 1.5 X versus 2 X carapace width), thinner and without spines on merus and carpus, merus elongate, propodus not expanded, no teeth on cutting edges of fingers; female abdomen oval, laterally elongate, with two submedial grooves; variable coloration, white, cream, brown and red, mottled, patched or plain, females more inconspicuously coloured; long setae on gastric and post-branchial regions of carapace surface, dense short setae on sternal surface and abdomen; males rarely exceeding 5.5 mm carapace width, mature females 3.0-5.5 mm carapace width.

MATERIAL EXAMINED: NEW SOUTH WALES: Eden, July, 1922, Livingstone and Fletcher, ♂, 3-4 miles off-shore, 20-30 faths (AM P.5795). VICTORIA: Type material listed above; Mordialloc, Port Phillip Bay, 2.vii.1897, Halliday, ♂ (tip of rostrum lost), 2 ov. ♀ ♀ (NMV); Beaumaris, Port Phillip Bay, 5.x.1901, ♀ , pres. S.W. Fulton, Sept. 1903 (NMV); Western Port Bay, Dec. 1905, C. J. Gabriel and J. H. Gatliffe, ♂, dredged (NMV); Lorne, 1917, A. Kenyon, ♂ (NMV); Western Port, Jan. 1967, K. Walker, 3 ♂ ♂, dredged from weedy channel, 10 feet (AM P.20171). TASMANIA: Derwent Channel, July, 1938, ♂, dredged (with *H. ovatus* and *H. innominatus)* (TM 15061/G301); D'Entrecasteaux Channel, 19.x.1964, J. Farnell, ♂, dredged (TM G956). WESTERN AUSTRALIA: Oyster Harbour, 22.viii.1963, B.R. Wilson and G. W. Kendrick, ♂, 2 ov. ♀ ♀, dredged near Green I. (WAM 2 lots); King George Sound, Dec. 1965, J. S. Lucas, ♂, 2♀ ♀ (AM P.20172); Emu Pt. Channel, Oyster Harbour, 10/11.vii.1966, J. S. Lucas, 14 ♂ ♂, 2 ov. ♀ ♀ , 9 ♀ ♀ , 5 im. ♀ ♀ (WAM); Rocky Bay, Swan River, 16.i.1973, P.N. Chalmer, 3♂ ♂(WAM).

## **HALICARCINUS BEDFORDI** Montgomery

Figs. 3A, 5E, 6N, 7G, 9E, 9F

*Hymenosoma* sp. — Montgomery, 1921:94-5.
*Halicarcinus bedfordi* Montgomery, 1931:425-6, pl. 27 figs. 3, 3a, b. — Melrose, 1975:82.

TYPE LOCALITY AND TYPES: Swan River, Western Australia. SYNTYPES: 1931 (presented), S. K. Montgomery, 3 ov. ♀ ♀ (4.0-4.5 mm, in poor condition) (BM 1931.7.24.35-6). Examined by Dr. R. W. Ingle (pers. comm.).

DISTRIBUTION: Northern and western Australia, as far south as the Swan River on the west coast and Moreton Bay on the east coast.

DIAGNOSIS: Rostrum approximately triangular, narrowing abruptly half-way or further along its length, terminating in a rounded point; eyes reaching to at least 0.4 length of rostrum; without a spine at posterior lateral angle; chelipeds massive and elongate in large males, 3 X or more carapace width; male abdomen almost equilateral triangular; male 1st pleopods with broad base and stout straight distal portion, terminating in a broad rounded point, with tufts of long setae arising subterminally.

DESCRIPTION: The following is additional to the description of Montgomery (1931) and the Diagnosis:— anterior lateral carapace angles hardly indicated, posterior lateral angles obtuse and rounded; rostrum slightly deflexed, concave in cross-section; rostral keel thin, continuous with interantennular septum; postocular lobes acute and prominent; antennal spines acute; two prominences in pterygostomial region, a large lobule or spine near base of cheliped and a smaller lobule or spine more anterior, these may be visible dorsally; ischium of 3rd maxillipeds slightly shorter than merus along lateral edge; chelipeds very enlarged and elongate in large males (Fig. 5E), merus of cheliped of large males with 3 distal spines, carpus with 2 distal spines, propodus progressively expanding towards fingers, fingers with wide gape proximally, distal third of fingers meet with finely serrated cutting edges, dactylus with basal tooth; chelipeds in females and small males less than 1.5 X carapace width, little thicker than walking legs; walking legs ca. 2 X carapace width, dactyli with small teeth along proximal ½-⅔ of length; female abdomen oval, strongly convex, with a medial ridge, segments 1-5 of increasing length and breadth, segments 1 and 2 visible dorsally, telson more than ⅓ total abdomen length, telson trapezoidal; eggs ca. 0.3 mm diameter; telson of male abdomen triangular with rounded apex, segment 5 longest segment in abdomen; colour pale brown; males up to 6.8 mm (Swan River) or 3.7 mm (other localities), mature females 4.0-6.7 mm (Swan River) or 3.2-3.8 mm (other localities).

REMARKS: Montgomery's description and illustration of the rostrum are misleading (Montgomery, 1931). The rostrum is only approximately triangular, it narrows abruptly half-way or futher along its length. The lateral rostral lobes are completly fused with the medial lobe and the point of narrowing is where they terminate. The terminal portion of the rostrum, consisting of medial lobe only, is longer and broader in specimens from Western Australia than from Queensland. The base of the rostrum is continuous with the acute postocular lobes over the bases of the eyestalks. Montgomery considered the postocular lobes to be the lateral rostral lobes.

*H. bedfordi* is a northern Australian species and the type locality, Swan River, W.A., is the southern-most locality of collection. It is usually rare in the Swan River: during four years of intensive collecting at this locality only one specimen was found (Lucas, 1968). However, in 1973 it was common in the shallows of the Swan River basin (P.N. Chalmer, pers. comm.). This followed several years of unusually mild freshwater discharge in the estuary. Specimens from the Swan River are larger than those from northern localities. Some females greater than 4 mm are immature and some males greater than 5 mm do not show the massive cheliped condition. At other localities the largest mature males and females do not reach these carapace widths.

MATERIAL EXAMINED: QUEENSLAND: Victoria Pt., Stns. 5 and 6, 12.ix.1962, F. C. Vohra, 2♂♂, im.♀, locality codes C96/62, CR 31/62 (QM W. 2350, W. 2355); Victoria Pt., 13.i.1963, F. C. Vohra, ♂ (1st pleopod mounted on slide) (AM P. 20180); Ross River, 8.vii.1970, J. S. Lucas, ov.♀, littoral, muddy substrate (JCU); Weipa, July 1972, W. McCormick, 3♂♂, 7 ov.♀♀ (AM P. 20167 (1♂); QM W. 4064); Moreton Bay, undated, 3♂♂, samples 795, 932, 1037 at locations 31A mud, 22A seagrass and 31C mud, respectively (CSIRO). WESTERN AUSTRALIA: Monkey Mia, Shark Bay, 8.viii.1967, T. D. Meagher, 2♂♂, ov.♀, in trawl net among dead *Posidonia australis* (WAM); Pt. Henry and Pelican Pt., Swan River, 10 and 18.i.1973, P. N. Chalmer, 11♂♂, 11 ov.♀♀, im.♀, 1 juv., on *Halophyla*, ½ m depth (WAM); Salters Pt., Swan River, 10.i.1973, P.N. Chalmer, 8♂♂, 10 ov.♀♀, im.♀ (AM P.20168).

### **HALICARCINUS INNOMINATUS** Richardson

*Halicarcinus planatus*. — Richardson, 1949a:68, fig. 48 (not *Cancer planatus* Fabricius, 1775).
*Halicarcinus innominata* Richardson, 1949b:130.
*Halicarcinus innominatus*. — Melrose, 1968:197, pl. 2 fig. 1; 1975:26-34, figs. 5-11, pl. 1C-F.
See Melrose (1975) for further Synonymy.

TYPE LOCALITY AND TYPE: Wellington Harbour (Melrose, 1975). Richardson (1949b) did not designate type specimens for the new species.

DISTRIBUTION: New Zealand, Chatham Islands, Stewart Island, Tasmania.

DIAGNOSIS: Carapace suboval, broader than long; rostrum arising well below carapace rim, rostral lobes short, subequal, close together, apically rounded, all pointing forward, lateral lobes at level of and not set at an angle to medial lobe; frontal carapace region not projecting; anterior and posterior carapace angles hardly evident, sometimes a small obtuse spine at position of posterior lateral angle; walking legs stout, dactyli with one row of teeth (based on Melrose, 1975).

DESCRIPTION: See Melrose (1975) for a comprehensive description. This is a large *Halicarcinus* species, with males up to 19 mm and mature females 7.5-15.5 mm; colour brown, with green or black tints (Melrose, 1975).

REMARKS: Specimens of *H. innominatus* from New Zealand were attributed to *H. planatus* until Richardson (1949b) recognized that they were another species, differing in features of the rostrum, lateral carapace angles and male chela. Garth (1958) reports Richardson's opinion that *H. planatus* is uncommon in New Zealand and that *H. innominatus* is the common species with which it has been confused. Gordon (1966) made a comprehensive study of the two species, giving further distinguishing features and concluding that *H. planatus* does not occur in New Zealand, but that is occurs south of the Chatham Islands (44°S) (see also Melrose, 1975). Subsequently, Lucas (1968) reported specimens of *H. innominatus* from Tasmania, where it is sympatric with the similar *H. ovatus*.

*H. innominatus* is unique among the Australasian marine hymenosomatids in having a trans-Tasman distribution. (One freshwater species, *Amarinus lacustris*, also occurs in Australia and New Zealand.) Generally, it appears that the Tasman Sea has acted as an effective geographical barrier between the Australian and New Zealand hymenosomatid faunas. Even the distribution of *H. innominatus* is most likely a recent phenomenon due to man's activities. Melrose (1975) reports that *H. innominatus* is found associated with the mussel *Perna canaliculus* (Martyn). This New Zealand mussel is present in Tasmania together with some other New Zealand marine invertebrates which are considered to have been introduced to Tasmania at various times after 1885 (Dartnall, 1969). The introductions apparently occurred with the importations of a New Zealand oyster, *Ostrea angasi* Sowerby, into Tasmania to bolster the Tasmanian oyster industry. In view of the close association of *H. innominatus* with *P. canaliculus* it is reasonable that they were both introduced to Tasmanian waters, either among the shipments of live oysters or from the keels of ships, which they inhabit (Melrose, 1975). The earliest record of *H. innominatus* from Tasmania is 1926.

MATERIAL EXAMINED: TASMANIA: Hobart Harbour, Derwent R. , Aug. 1926, M. Ward, ♂, from wharf piles (AM P.8646); Georges Bay, NE coast, 10.ii.1927, T. T. Flynn, 2♂♂ 3-4.5 faths (AM P.9242); Derwent Channel, July 1938, ♂, dredged (with *H. ovatus* and *H. rostratus*) (TM 15061/G301); Roches Beach, Frederick Henry Bay, 26.ii.1964, J. Greenhill, ♂, ov. ♀, midlittoral zone on rocky reef (with *H. ovatus*) (TM 19015/G652).

## **HALICARCINUS HONDAI** (Takeda and Miyake)

Figs. 3H, 6O, 7H, 9K

*Rhynchoplax hondai* Takeda and Miyake, 1971b:168-70, fig. 3. — Sakai, 1976:149-50.

TYPE LOCALITY AND TYPE: Omonawa, Tukuno-shima I., Ryukyu Is., Japan. HOLOTYPE: 22.viii.1968, K. Honda and M. Takeda, ♀ (1.9 mm) (ZLKU 13088).

DISTRIBUTION: Ryukyu Is., Japan, and Townsville, Australia.

DIAGNOSIS: Medial lobe of rostrum long and narrow, far outreaching eyes, length ¼-⅓ carapace width, with one or more long setae terminally, lateral lobes not evident, completely fused with medial lobes, making broad base of rostrum; eyestalks elongate, with a prominence on medial edge; female abdomen broader than carapace width, conspicuous laterally and posteriorly in dorsal view, segments 3 and 4 fused without suture evident.

DESCRIPTION: The following data supplement the description of Takeda and Miyake (1971b), who only had access to the immature female holotype:— carapace width to length (excluding rostrum) ratio 1.21 (♂) and 1.37 (ov.♀); rostral keel and antennal spines absent; ischium of 3rd maxillipeds subequal to merus along lateral edge; chelipeds of male and female ca. 1½ X carapace width, female chelipeds slightly stouter than walking legs, male chelipeds stouter than female, with a prominent tooth distally on merus and carpus, propodus inflated, fingers 0.4 X total propodus length, dactylus with large basal tooth, fingers with serrations along distal cutting edges; walking legs ca. 2 X carapace width, stout, with large tooth on dorso-distal edge of merus, dactylus curved, without teeth proximally, with a row of teeth increasing in size distally; female abdomen very large, widest at junction of segments 4 and 5, segments 1 and 2 short, fused segments 3 and 4 together longer than segment 5 and shorter than telson, telson trapezoidal; female pleopods projecting laterally from abdomen; eggs 0.23 mm diameter (?) (one only), ovaries appear to extend into abdomen; male abdomen elongate triangular, segments 3 and 4 fused and no suture evident, telson spade-shaped; male 1st pleopod with thinner portion arising at ca. 90° from stout base, bending through ca. 90° again a short distance above base and then slightly curved, tapering to a concave tip distally; colour off-white, pale orange; scattered long setae on dorsal carapace surface and legs; mature individuals less than 3 mm.

REMARKS: The two specimens of *H. hondai* collected from reefs near Townsville, Great Barrier Reef region, show only minor differences from the female holotype and they do not warrant separate taxonomic status without examination of further specimens. The male, but not the female specimen, from the G.B.R. region shows stronger grooves on the dorsal carapace surface than the female holotype; and the rounded prominence on the eyestalk and blunt pterygostomial tooth of the holotype are acute teeth in the G.B.R. specimens. The two widely separated localities where *H. hondai* has been collected suggest that it has a wide geographical distribution in the western Pacific. Because of its very small size it has probably escaped being noticed and collected.

The disproportionate size of the mature female abdomen and projecting pleopods of *H. hondai* are to increase its egg-carrying capacity. This phenomenon also occurs in another minute *Halicarcinus* species, *H. keijibabai*, and in two minute *Elamena* species, *E. gordonae* and *E. umerata*. Fusion of segments in the female abdomen of *H. hondai* may be related to the expansion of the abdomen or lateral projection of the pleopods. This fusion also occurs in *H. afecundus* n.sp., *E. umerata* and possibly in *E. gordonae*, but not in *H. keijibabai* (as figured, but not described, by Takeda and Miyake, 1971b). *H. afecundus* n.sp. does not have an expanded female abdomen, but it has large eggs and the fusion of abdominal segments probably relates to its particular mode of reproduction. These fusions of segments occurring in a few species of *Halicarcinus* and *Elamena*, genera which otherwise show no fusion of female abdominal segments, are considered to be specific adaptations to very small size or a particular mode of reproduction. The condition has arisen independently in each species, i.e. they are analogous conditions, and it is not considered to be of phylogenetic significance.

The single egg on the *H. hondai* female is very small, even by hymenosomatid standards. It may be a prematurely released egg, as the female was in an aquarium for several days before being preserved. If it does represent the normal size of eggs of this species, the zoea emerging must be at, or very near, the end of the scale of small brachyuran zoeae.

It appears that segments 3 and 4 in the male abdomen of *H. hondai* are also fused. In all of these small species with fused abdominal segments it is desirable to have a series of specimens, as it is not easy in some specimens to distinguish sutures from articulations. However, in the sole male specimen of *H. hondai*, not even a suture can be seen between segments 3 and 4 (Fig. 7H), so the condition seems clear. This may be linked with fusion of segments in the female abdomen and it would be interesting to examine males of *H. afecundus* n.sp. to see if they also show fused segments.

MATERIAL EXAMINED: Picnic Bay, Magnetic Island, Queensland, Australia, 8.viii.1972, J. S. Lucas, ♂ (1.93 mm, 1st pleopod detached and mounted on a slide), on coral in intertidal zone (QM W.4068); Townsville, Queensland, Australia, Dec. 1973, J. S. Lucas, ov. ♀ (2.64 mm, carrying only one egg), on coral rubble from patch reef (QM W.4067).

## **HALICARCINUS AFECUNDUS** n.sp.

Figs. 3G, 6M

TYPE LOCALITY AND TYPE: Lindeman Island, Cumberland Island Group, Queensland, Australia. HOLOTYPE: 5.ix.1935, ov. ♀ (5.4 mm) trawled in 10 faths (AM P.12225).

DIAGNOSIS: Rostrum arising slightly below carapace rim, lobes well spaced, lateral lobes distinctly longer and broader than medial lobe, medial lobe slightly deflexed, lateral lobes sloping up; eyes short, little visible dorsally; female abdomen with segments 2-5 fused and sutures inconspicuous; eggs ca. 0.7 mm diameter.

DESCRIPTION: Not including male features:— carapace subcircular, ratio of carapace width to length (including rostrum) ca. 1.08; dorsal carapace surface with a discontinuous medial longitudinal ridge, gastro-cardiac, cervical and thoracic grooves well defined, other grooves faint; lateral carapace walls sloping out ventrally; anterior lateral carapace angles with an obtuse spine, posterior lateral angles obtuse and rounded, a prominent acute spine slightly posterior and below posterior lateral angle; postocular lobes small; interantennular septum well developed; no rostral keel; no antennal spines; pterygostomial regions with an acute spine near base of cheliped, two obtuse lobes anterior to it; ischium of 3rd maxilliped subequal with merus along lateral edge; female chelipeds slightly stouter than walking legs, length 1¼ X carapace width; fingers half total propodus length, fingers with fine serrations, curved distally; walking legs slender, longer than 2X carapace width, dactyli little curved, long and tapering, with two small teeth subterminally; female abdomen oval, convex, telson longest segment, ca. ⅓ total abdomen length; female genital apertures laterally elongate (related to large egg size); eggs few in number, 5.4 mm female carries 24 eggs; female strongly setose around border of abdomen and on legs.

REMARKS: Although no male specimens of *H. afecundus* were seen, the sole female specimen is very distinctive and clearly a new species. It is one of three *Halicarcinus* species in which the lateral rostral lobes are longer than the medial lobe; but, whereas in *H. planatus* and *H. tongi* the lateral lobes are slightly longer, in *H. afecundus* they are twice as long as the medial lobe in the type specimen. *H. afecundus* does not appear to be closely related to *H. planatus* or *H. tongi*. It belongs with the *Halicarcinus* species with well-spaced rostral lobes and most resembles *H. minutus* and some specimens of *H. ovatus*. It is unusual among *Halicarcinus* species in having fused segments in the female abdomen. This character is also shown by *H. hondai*.

The eggs of the *H. afecundus* female are twice the diameter of most other *Halicarcinus* species and it is very probable that this species has suppressed or abbreviated larval development. For comparison: *Amarinus lacustris*, with no free larval stages, carries eggs of 0.7 mm diameter; its sibling species, *A. paralacustris*, with normal larval development, carries eggs of 0.35 mm diameter (Lucas, 1970). The number of eggs in each egg mass is reduced as a consequence of the larger egg size, so that the *H. afecundus* female carries only 24 eggs. Similar sized females of *Halicarcinus ovatus* and *Amarinus paralacustris* (normal larval development) carry ca. 530 and 280 eggs, respectively, while a 5.4 mm female of *A. lacustris* (suppressed larval development) carries ca. 35 eggs (Lucas, 1968, from Fig. 5.13) (see also Table 4). Suppression or abbreviation of free larval development involves a prolongation of embryonic development as well as increased egg size.

Another marine hymenosomatid, *Elamenopsis bovis* (which also occurs in brackish water), is known to have suppressed larval development. The phenomenon is uncommon among marine Brachyura and only known from three other families (see section on Reproductive strategies). An advantage of suppressing or abbreviating larval stages is that it reduces the mortality of the young stages through unfavoural dispersal and exposure to predators of plankton. Disadvantages are reduced dispersal of the offspring and lowered fecundity, because of the need to produce larger eggs supporting longer embryonic development. Other adaptations of hymenosomatid females to compensate for the low fecundity imposed by their small size are considered in the section on Reproductive strategies.

The name *afecundus* (not fecund; Latin, masculine) refers to the small number of eggs carried by the female holotype.

MATERIAL EXAMINED: Holotype.

## **TRIGONOPLAX** H. Milne Edwards, 1853

*Trigonoplax* H. Milne Edwards, 1853:224 (type species, by monotypy, *Ocypode (Elamene) unguiformis* de Haan, 1839:75-6, pl. 29 fig. 1 and pl. H (called *Inachus (Elamene) unguiformis* in pl. H)).

DIAGNOSIS: Carapace approximately triangular; anterior lateral angles almost absent, antero-lateral borders very long; carapace surface without well defined grooves; rostrum rounded triangular, not defined or poorly defined from carapace surface, concealing antennules, antennae and most of eyes; rostral keel present; epistome very long and bulging; Milne Edwards apertures fused laterally for more than half their length; mouth-field approximately square, completely filled by 3rd maxillipeds; ischium of 3rd maxilliped subequal or longer than merus along lateral edge; chelipeds similar in both sexes, not thicker than walking legs; walking legs long and slender, dactyli with one or two subterminal teeth; female abdomen broad, weakly convex; male abdomen broad, without fused segments; male 1st pleopods curved, bearing a subterminal row of long setae.

SPECIES OF *TRIGONOPLAX*:

| **Species** | **Distribution** |
|---|---|
| *T. unguiformis* (de Haan, 1839) | Japan; Singapore; Ternate;<br>G. of Martaban; Andaman Is.;<br>Natal |
| *T. longirostris* McCulloch, 1908 | southern Australia |
| *T. spathulifera* n.sp. | northern Australia |

REMARKS: *T. unguiformis* differs markedly from the *Elamena* species with truncate rostra, e.g. *E. mathaei*, in the form of the carapace, rostrum, rostral keel, and epistome — differences which were recognized by early workers. However, with the discovery in India of several species of apparently intermediate form, which were included in the *Trigonoplax* taxon, the differences between *Trigonoplax* and *Elamena* were considered to be trivial and the former at best a subgenus (Alcock, 1900, Kemp, 1917).

*Trigonoplax* is recognized here as a genus with three similar species which are readily distinguished from all *Elamena* species by their unique partially-fused Milne Edwards apertures (Fig. 5F), almost straight anterior lateral angles, long antero-lateral carapace borders and very long epistome. There are probably at least several other undescribed species, e.g. *T.* species of de Man (1902) and *E. (T.) unguiformis* of Alcock (1900) and Kemp (1917). Specimens from various Indo-West Pacific localities, which have been attributed to *T. unguiformis*, vary in features such as carapace width to length ratio, rostrum, rostral keel, cheliped fingers, size of the terminal spine on the merus and shape of the dactylus of walking legs, and number of segments in the male abdomen (?).

Larval morphology provides further support for the separate generic status of *Trigonoplax* and *Elamena*. As discussed in the Remarks on the genus *Elamena*, larvae of a number of *Elamena* species have been described and they are characterized by unique lateral expansions of the abdomen and very short rostrum, antennae and antennules. The first stage zoea of *T. unguiformis* from Japan, described by Aikawa (1929), has a normal abdomen and moderate-sized rostrum, antennules and antennae.

MATERIAL EXAMINED: (Other than Australian material) *T. unguiformis:* Japan, undated, ♀, Old Collection (stuck to glass plate) (AM P.139); Inland Sea, Japan, undated, ♂ (BM 1907.4.27.5). (Seven dried syntypes of *T. unguiformis* in the Rijksmuseum van Natuurlijke Historie, Leiden, were recently examined by Dr L. B. Holthuis (pers. comm.).)

### **TRIGONOPLAX LONGIROSTRIS** McCulloch

Figs. 5A, B, F, H, 6A, 8A, 9I, J

*Elamena (Trigonoplax) unguiformis.* — Fulton and Grant, 1906a: 10-11, fig. (not *Ocypode (Elamene) unguiformis* de Haan, 1839).

*Trigonoplax unguiformis* var. *longirostris* McCulloch, 1908:59, pl. 12 fig. 3 — Kemp, 1917:278.

*Trigonoplax unguiformis longirostris.*— Tesch, 1918:26.

*Elamena (Trigonoplax) unguiformis* var. *longirostris.* — Hale, 1924:70-1, fig. 1.

*Elamena (Trigonoplax) unguiformis longirostris.*— Hale, 1927:120-1, fig. 118.

*Trigonoplax unguiformis.* — Griffin, 1972:66-7 (not *Ocypode (Elamene) unguiformis* de Haan, 1839).

TYPE LOCALITY AND TYPES: Western Port, Victoria (not Port Phillip, Victoria, given by McCulloch (1908)). SYNTYPES: undated, T. Gabriel, ♂ (9.0 mm), ♀ (15.2 mm), labelled as types of *Trigonoplax unguiformis* var. *longirostris* (AM P.12). The female is the same size as that figured by McCulloch and is hereby designated lectotype of *Trigonoplax unguiformis longirostris* McCulloch, 1908.

DISTRIBUTION: Southern Australia, excluding Tasmania, from Mandurah on the west coast to Western Port on the south-eastern coast.

DIAGNOSIS: Carapace width to length ratio approximately 1.0, less than 1.1; rostrum often deflexed; rostral keel shallow, not nearly reaching tip of rostrum; lateral walls of carapace strongly converging ventrally; fingers of chelae weakly spatulate; dactyli of walking legs distinctly broadest medially.

DESCRIPTION: Carapace width to length ratio 0.97-1.06 (Fig. 5A); carapace surface generally concave, with a slight rim, without grooves; lateral walls of carapace shallow; branchial regions of carapace projecting out over ischia of walking legs 1-3; rostrum elongate triangular with rounded sides and apex, laterally concave in dorsal view, separated from carapace by a slight ridge, level with carapace surface or slightly deflexed (Fig. 5B); rostral keel continuous with prominent interantennal septum; eyes short, eye-stalks very broad and flattened; postocular lobes generally visible dorsally; basal antennular segment with a distal lateral spine; no antennal spines; pterygostomial region simple; length of chelipeds ca. 1¼ X carapace width, fingers with small teeth along most of cutting edges, slightly curved and spatulate, only meeting at tips, 0.4 X propodus length (Fig. 5H); merus of each walking leg with a distal spine; length of walking legs 2½ X carapace width in large specimens, greater in small specimens, each dactylus distinctly broadest medially, about as broad as merus of same leg; 5th segment longest segment of female abdomen; male abdomen broad at segments 1-3, constricting sharply at segment 4; male 1st pleopod strongly curved, not very stout at base, with a subterminal row of 7-10 large setae; setation restricted to borders of Milne Edwards apertures, mouthparts and dactyli of walking legs; colour brown, yellow or yellow-green; largest male 12.7 mm, mature females 12.9-16.8 mm.

REMARKS: McCulloch (1908) considered that *T. u.* var. *longirostris* was probably a species, but since he had only four specimens he preferred to regard it as a variety. This original status of *T.u.* var. *longirostris* is to be regarded as subspecific, according to I.C.Z.N. (1961) Article 45(d) (ii) and (e), and it is here elevated to species. Characters by which McCulloch distinguished *T. u. longirostris* from *T. unguiformis*, carapace width to length ratio approximately 1.0, compared to a ratio of ca. 1.2, and distinct medial broadening of the dactyli of the walking legs, are consistent in all specimens of *Trigonoplax* from southern Australia.

*Trigonoplax longirostris* McCulloch is invalid if *Trigonoplax* is treated as a subgenus of *Elamena* H. Milne Edwards. *Elamena (Trigonoplax) longirostris* (McCulloch) is a junior secondary homonym of *Elamena longirostris* Filhol 1885a, notwithstanding the fact that the former is in the subgenus *Trigonoplax*, I.C.Z.N. (1961) Article 57(a). *E. unguiformis longirostris* (McCulloch), used by Hale (1927), is also a junior secondary homonym.

MATERIAL EXAMINED: VICTORIA: Syntypes listed above; Shoreham, 10.xi.1902,♂ (NMV); Rhyll, Western Port, May 1906, J. Gabriel, 3♂♂, 2♀♀ (these specimens were examined by Fulton and Grant (1906a) and the largest male specimen was figured) (NMV); Shoreham, undated, S. W. Fulton,♂(NMV). SOUTH AUSTRALIA: Port Vincent, 8.ii.1949, M. Bonnin,♀(SAM C.3159). WESTERN AUSTRALIA: Emu Point Channel, Albany, 10/11.viii.1966, J. S, Lucas,♀, dredged from sublittoral (WAM); Mandurah, undated, ov.♀, 402/40 (WAM).

## **TRIGONOPLAX SPATHULIFERA** n.sp.

Figs. 5C, D, I, 6B, 8F, 9G

TYPE LOCALITY AND TYPES: Bushy Island, Queensland. HOLOTYPE: im.♀ (7.5 mm, right cheliped detached), collected from a reef at Bushy Island (50 miles east of Mackay, Q.), 1938, F. A. McNeill (AM P.11465). PARATYPES: QUEENSLAND: St. Crispin Reef, off Port Douglas, 1918, A. R. McCulloch, im.♀(the specimen referred to by E. W. Bennett in his 10.xii.1929 letter; walking legs mutilated or absent) (AM P.4307); Nor'West Islet, Capricorn Group, April 1933, F. A. McNeill,♂(1st pleopods detached, one mounted on slide) (AM P.10363); 21°43'S, 152°25'E, NW end of Gillett Cay, Swain Reef Expedition, Stn 1, 1962, Aust. Musuem Party, ♂ (AM P.17011); One Tree Island, Capricorn Group, 25.ix.1965, F. H. Talbot, ov.♀ (AM P.15985); Heron Island, Capricorn Group, undated, A. Cameron, ov. ♀ (AM P.11376). WESTERN AUSTRALIA: Delambre Island, 9.vi.1960, B. R. Wilson, ov.♀, collected from coral reef, under a stone at low tide (WAM); Mary Ann Reef Buoy, Mary Ann Passage, 17.vii.1963, R. J. Hannan,♀ (WAM); Pt. Hedland, Nov. 1963, G. Beamish, ov.♀, on reef (WAM); 30°00'S 114°28'E, NW of Jurien Bay, 28.i.1964, ov.♀, beam trawl, 70-75 faths, from sponge and bryozoa, DM 1/64 (WAM).

DISTRIBUTION: Northern Australia, from Lancelin Island on the west coast to Gladstone on the east coast.

DIAGNOSIS: Carapace width to length ratio 1.1-1.3; rostrum often strongly upturned; rostral keel deep, extending for full length of rostrum, generally visible dorsally; lateral walls of carapace approximately vertical; fingers of chelae strongly spatulate; dactyli of walking legs varying little in breadth before curved terminal portion.

DESCRIPTION: Carapace surface generally convex, irregular but without distinct grooves, with a distinct rim (Fig. 5C); branchial margins of carapace not overlying ischia of walking legs; posterior lateral angles sometimes with pronounced points; rostrum triangular with rounded sides and apex, varying from level with carapace surface to strongly upturned, laterally concave, flat or convex, not completely concealing antennules dorsally (Fig. 5D); rostral keel usually visible dorsally; postocular lobes small and inconspicuous; basal antennular segment with a small lateral spine distally; epistome shorter than mouth-frame; pterygostomial region with a small ridge; cheliped length ca. 1¼ X carapace width; fingers with fine teeth and some large teeth along most of cutting edges, curved and strongly spatulate, ca. 0.5 X propodus length (Fig. 5I); merus of each walking leg with a prominent distal spine, second walking leg 2½ X carapace width in large specimens, 3 X in holotype and greater in small specimens; telson longest segment of female abdomen; male abdomen broadest at segments 1-3, constricting at segment 4 (see Remarks); setation only on Milne Edwards apertures, mouthparts, dactyli of walking legs and inner surfaces of fingers; largest male 3.6 mm (probably immature), mature females 8.4-14 mm.

REMARKS: The name *spatulifer* was originally suggested by E. L. Bennett. In a letter in the Australian Museum files, dated 10.xii.1929, he proposed a female specimen, AM P.4307, as holotype of a new species, *T. spatulifer,* but never subsequently published a description. This female specimen was one of a number of specimens of an undescribed species from northern Australia examined during this study and as "spatulifer" is an appropriate descriptive name for this species, it is used here. Its correct form is *spathulifera,* flat blade bearer (Latin, feminine), referring to the fingers of the chelae. The specimen proposed as a holotype by Bennett is in poor condition and another holotype is chosen.

It is unusual that only two of nine specimens of *T. spathulifera* in Australian museum collections are males and that these males are much smaller than the smallest female specimen. The males are probably immature, thus the abdomen and 1st pleopod figured (Fig. 8F and 9G) probably represent an immature condition of these structures. They cannot be used for comparison with *T. longirostris.*

MATERIAL EXAMINED: Type material listed above.

## **ELAMENOPSIS** A. Milne Edwards, 1873

*Elamenopsis* A. Milne Edwards, 1873:324 (type species, by monotypy, *Elamenopsis lineatus* A. Milne Edwards, 1873).

*Neorhynchoplax* Sakai, 1938: 194, 200 (type species, by subsequent designation of Holthuis (1968), *Rhynchoplax introversus* Kemp, 1917; this species has precedence over *Rhynchoplax alcocki* Kemp, 1917 designated as "genotype" of *Neorhynchoplax* by Sakai (1976)).

DIAGNOSIS: Carapace approximately circular, octagonal or hexagonal; dorsal carapace surface with well defined grooves, with rim continuous across base of rostrum; rostrum generally tridentate or trilobate; epistome short, breadth exceeding 2 X length; pterygostomial regions plain; 3rd maxillipeds narrow and well separated, ischium shorter than merus along lateral edge; sternal region projecting forward between bases of 3rd maxillipeds; chelipeds stouter than walking legs, especially in large males; dactyli of walking legs often with a subterminal tooth or row of teeth; female abdomen with segments 3-5 fused, without pleopods, with a brood cavity within abdomen and posterior cephalothorax (not described in many species); male abdomen with segments 3-5 or 4-5 fused (or no segments fused?); male 1st pleopods with a stout base and thinner distal portion, curved towards sternum distally, with light setation (not described in many species).

SPECIES OF *ELAMENOPSIS:* Based on A. Milne Edwards (1873), Sakai (1938, 1969), Barnard (1946), Wu et al. (1962) and Takeda and Miyake (1971a).

| **Species** | **Distribution** | **Habitat** |
|---|---|---|
| *E. lineata* A. Milne Edwards, 1873 | New Caledonia; Queensland; Philippines | brackish-marine |
| *E. woodmasoni* (Alcock, 1900) | Andaman Islands; West Bengal, India; Sri Lanka | marine |
| *E. inachoides* (Alcock, 1900) | West Bengal, India | marine |
| *E. alcocki* (Kemp, 1917) | West coast, India | brackish |
| *E. octagonalis* (Kemp, 1917) | Goa, India; Queensland, Australia | brackish-marine |
| *E. demeloi* (Kemp 1917) | Goa, India | brackish |
| *E. exigua* (Kemp, 1917) | Thailand | brackish |
| *E. introversa* (Kemp 1917) | Kiangsu Prov., China | fresh water |
| *E. nasalis* (Kemp 1917) | West Bengal, India | brackish |
| *E. kempi* (Chopra and Das, 1930) | Basra, Iraq; Panama Canal | fresh water |
| *E. tuberculata* (Chopra and Das 1930) | Cochin, Travancore, India; Sri Lanka | fresh-brackish |
| *E. sinensis* (Shen, 1932) | Shantung Pen., China | marine |
| *E. bovis* (Barnard, 1946) | South Africa | brackish-marine |
| **E. species* (Wu et al., 1962) | Shihlin, Taiwan | brackish |
| *E. ariakensis* (Sakai, 1969) | Nagasaki Pref., Japan | marine, commensal |
| *E. inermis* (Takeda and Miyake, 1971a) | Palau Islands | fresh water |
| *E torrensica* n.sp. | Torres Straits, Australia | brackish-marine |
| *E. aspinifera* n.sp. | N. Queensland, Australia | brackish-marine |

*Not adequately described for identification as a new species or as an already described species.

REMARKS: Sakai (1938) separated a number of the Indian hymenosomatids previously included in *Rhynchoplax* Stimpson, 1858, into a new genus *Neorhynchoplax* Sakai, 1938. He did this on the basis of their slender 3rd maxillipeds and fusion of segments 3-5 in the male abdomen. However, *Elamenopsis lineata* is congeneric with the *Neorhynchoplax* species and *Elamenopsis* is the oldest valid generic name. *E. lineata* is most closely related to the group of *Elamenopsis* species which have short rostra, especially short lateral lobes, and little dentation of the walking leg dactyli, and which tend to have laterally compressed walking legs. These species are *E. demeloi, E. tuberculata, E. ariakensis* and *E. inermis.*

Two species included by Sakai (1938) in *Neorhynchoplax* are excluded from the list of *Elamenopsis* species given here. They are *Hymenicus krefftii* Hess, 1865 and *Elamena filholi* de Man, 1887b. (See Remarks on the genus *Halicarcinus* for discussion of these species.)

In the four *Elamenopsis* species occurring in Australia and in the two Indian species examined at the British Museum the abdominosternal morphology of mature females is most unusual. It is unique among hymenosomatids and possibly among Brachyura. The female abdomen bears no pleopods and the abdominosternal cavity is reduced to a minimum. Instead of being carried on pleopods, eggs are brooded in an internal cavity within the abdomen and the posterior portion of the cephalothorax (Fig. 8H). The fused sternites of the abdomen (Fig. 5J) consist of very thin cuticle which is well separated from the fused tergites. This allows one layer of eggs between the sternites and tergites of the abdomen. The sternite cuticle of the abdomen is connected to the sternum of the cephalothorax from about the level of the 3rd walking legs, behind the genital apertures. If the abdomen is lifted away from the cephalothorax, the abdomen sternite cuticle is torn away from the cephalothorax sternum. In the intact mature female the brood cavity within the abdomen is continuous with a cavity extending into the posterior portion of the cephalothorax. Eggs are visible in this cavity through the dorsal surface of the carapace, at least in preserved ovigerous females. Apparently the eggs are not extruded through the genital apertures but remain within the body. This poses the problems: How are the eggs irrigated for gaseous exchange, etc., during development and how are larvae released? It appears that larvae can only be released by rupturing the thin sternites and cuticle at some point. Two ovigerous females of *E. lineata* and one of *E. aspinifera* n.sp. released larvae while maintained in the laboratory. These were normal first stage zoeae and no abnormalities in the female reproductive structures were suspected at the time.

Most authors have reported ovigerous *Elamenopsis* females without commenting on

Note added in press:

Serene (1971) described a new species, *Neorhynchoplax palawensis,* from the Philippines. Serene's brief description does not include diagnostic features such as 3rd maxillipeds, but it is probably an *Elamenopsis* species. It has laterally compressed walking legs, like *Elamenopsis* species such as *E. demeloi,* unusually elongate lateral rostral lobes and a unique pair of lobes projecting posteriorly from the 1st segment of the male abdomen.

Serene R. 1971. Observations preliminaires sur des Brachyoures nouveaux ou mal connus du Sud-Est Asiatique (Crustacea Decapoda). *Bull. Mus. Hist. nat., Paris* (ser. 2) 42(5): 903-918.

the female reproductive system. However, Shen (1932) figured the female abdomen of *E. sinensis,* from China, showing the characteristic segment fusion and shape, and Wu et al., (1962) noted that the abdomens of both sexes of a species of *Elamenopsis* from Taiwan were composed of four segments. Thus, as the six species examined in detail in this study are representative of the range of *Elamenopsis* species and as fused abdominal segments in females are known for two other species, it is very probable that the unique female reproductive morphology is characteristic of the genus *Elamenopsis.*

In addition to female morphology, *Elamenopsis* is notable for the number of euryhaline species, for three species permanently inhabiting fresh water, and for a commensal species of hymenosomatid, *E. ariakensis,* which is commensal with a holothurian (Sakai, 1969). *Elamenopsis* species differ markedly in morphology from the other group of hymenosomatids in brackish and freshwater habitats, *Amarinus* n. gen. species, in having narrow 3rd maxillipeds, usually tripartite rostra and in fusion of abdominal segments. *Elamenopsis* is mainly a northern hemisphere genus and *Amarinus* n. gen. is mainly in the southern hemisphere, their distributions overlap along the Queensland coast in Australia.

MATERIAL EXAMINED: (other than Australian species) *Elamenopsis alcocki:* Portuguese India, undated (Sept. 1916?), 2 ♂♂, 2 ov.♀♀, labelled *"Rhynchoplax alcocki* cotypes" (BM 1919.11.1.117-120). *Elamenopsis* species *(demeloi?):* Kuda Kalapu ganga, Randombo, Ceylon, C. H. Fernando, 29.viii.1954, ♂♂ and ♀♀ (BM).

## **ELAMENOPSIS LINEATA** A. Milne Edwards

Figs. 3J, 5J, 8E, 10J

*Elamenopsis lineatus* A. Milne Edwards, 1873:324-5, pl. 18 fig. 4. — Kemp, 1917:250. — Tesch, 1918:26-8, pl. 1 figs. 5, 5a-c. — Serene and Umali, 1970:58, pl. 5 fig. 11.

TYPE LOCALITY AND TYPE: Dotio, New Caledonia (in brackish water); HOLOTYPE: ovigerous female, not a male as stated by A. Milne Edwards (1873), in Muséum d'Histoire Naturelle, Paris (J. Forest, pers. comm.).

DISTRIBUTION: New Caledonia, northeastern Australia, Philippines.

DIAGNOSIS: Carapace wider than long, approximately hexagonal; rostrum triangular with rounded apex, strongly deflexed and nearly perpendicular; walking legs broad and laterally compressed, dactyli without teeth; male abdomen with segments 4 and 5 fused and suture indistinct or without fused segments (? — see Description).

DESCRIPTION: Tesch (1918) gave a full description of a male specimen of *E. lineata* and generally the Australian material agrees with Tesch's description. In Australian specimens the dorsal carapace surface is slightly concave rather than "perfectly flattened" as in Tesch's specimen and the abdomens of male specimens from Australia have segments 4 and 5 fused (Fig. 8E), while Tesch figures a male abdomen apparently without fused segments. There is still a faint suture evident at the fusion of segment 4 and 5 in some Australian males and it is possible that this is the condition in Tesch's male. The male 1st pleopod, which was not described by Tesch (1918), has a stout base and then tapers to a rounded tip (Fig. 10J). The terminal portion is curved and has a strong ridge on the sternal side. There are scattered short setae near the tip and a few long setae arising just before the curved terminal portion.

Female features are: chelipeds similar to but smaller than those of males, only slightly stouter than legs; abdomen convex, segment 1 widest, segments 2-5 of similar width, telson triangular and much narrower than previous segments (Fig. 5J); sternum distinctly contoured to receive close-fitting abdomen and telson, with two small projections over abdomen at level of segment 5.

Largest male and female 3.3 and 3.8 mm, respectively; coloured dark brown.

REMARKS: There have been three previous reports of *E. lineata,* each involving a single specimen. However, this species is quite common in certain habitats in the Victoria Point-South Dunwich area, south of Brisbane, as evidenced by the number collected and deposited in the Queensland Museum during a survey in 1962. *E. lineata* has been collected on a number of occasions in Ross River, Townsville, by digging in a muddy substrate, and its distinctive larvae are common in plankton samples from Ross River and the Johnstone River, north of Townsville. It has largely escaped notice because its size, coloration and behaviour make it very inconspicuous. With the apparent exception of Tesch's specimen from "on the coral reefs, at Sangir, north of Celebes", "Siboga" Expedition Stn 127 (129?) (Tesch, 1918), the localities where *E. lineata* has been collected are estuaries or coastal localities subject to brackish salinities. "Coral reefs" seem to be an unlikely habitat in view of the other reports.

The zoeae of *E. lineata* are like the zoeae of other hymenosomatids inhabiting brackish water in having well developed carapace spines. The zoeae of *E. lineata* are particularly like those of *Hymenosoma orbiculare,* with elongate rostral and mid-dorsal spines; but these spines in *E. lineata* are extremely elongate, being approximately three times and two times the carapace length, respectively, in the first stage zoea (Lucas, unpublished data). This makes the zoea very distinct among hymenosomatid zoeae and brachyuran zoea generally. Another less conspicuous but distinctive feature of *E. lineata* zoeae is the presence of two setae on the coxal endite of the 2nd maxilla. In other hymenosomatid species in which this larval appendage has been described there is only one seta on the coxal endite.

MATERIAL EXAMINED: QUEENSLAND: Manly, Moreton Bay, 27.vii.1946, J. S. Hynd, ♂, from mud, *Zostera* (AM P.12204); South Dunwich, 15.vii.1962-14.x.1962, J. F. Vohra, 7 ♂♂, 2 ov.♀♀, ♀, 2 im.♀♀, Stns 3, 6 and 7, *Zostera* (QM W.2337, W.2341, W.2342, W.2343, W.2346); Victoria Pt., 12. ix.1962 and 11.x.1962, F. C. Vohra, 3♂♂ Stns 3 and 5 (QM W.2338, W.2353); Ross River, Townsville, Jul. 1969 and 2.x.1970, J. S. Lucas, 2♂♂ 2 ♀♀(both females released larvae then moulted in laboratory) (JCU); Weipa, Jul. 1972, W. McCormick, im. ♀, benthos off mangroves (AM P.20170); Dunwich, Moreton Bay 4.v.1973, J. S. Garth, ♂, ♀, sandy mud flats with turnable rocks (with *E. octagonalis)* (AHF JG9-73).

### **ELAMENOPSIS OCTAGONALIS** (Kemp)

Figs. 4A, 6P

*Rhynchoplax octagonalis* Kemp, 1917:256-8, fig. 5.
*Neorhynchoplax octagonalis.*— Sakai, 1938:2.

TYPE LOCALITY AND TYPE: Vareeg Islet, Mormugao Bay, Goa, India. HOLOTYPE: ov. ♀(3.9 mm, carapace length) (Indian Museum, Zoological Survey of India No. 9740/10).

DISTRIBUTION: Goa, India; Queensland, Australia.

DIAGNOSIS: Carapace approximately octagonal; lateral carapace walls with a forward directed spine above base of 1st walking leg; rostrum consisting of three separate spine-like lobes, fringed with short setae, lateral lobes well spaced from medial lobe and pointing slightly upward and outward, medial lobe longest and pointing forward; walking legs not laterally compressed, dactyli with one subterminal tooth; male 1st pleopod terminating in a long thin point.

DESCRIPTION: The following is additional to the description of the female holotype by Kemp (1917) and the Diagnosis: — carapace width to length ratio (excluding rostrum) 0.93-1.07 (Australian specimens) (Fig. 4A); basal antennular segment with strong lateral tooth; no rostral keel; antennal spines small and obtuse; pterygostomial regions with strong ridge dorsally; length of male chelipeds 1½ carapace width, merus with a subterminal tooth ventrally, propodus inflated, particularly expanded ventrally, propodus depth ca. 1.8 mm in 3.4 mm male, fingers each with a row of ca. 7 teeth which fit together when fingers close, fingers curved distally; length of female chelipeds slightly greater than carapace width, stouter than walking legs but much smaller than male chelipeds; telson of female abdomen small, difficult to distinguish from segment 5 and possibly fused to it; male abdomen narrow, segments 3-5 fused without sutures, fused article and telson elongate, similar to *E. demeloi* (see Kemp, 1917, Fig. 9); male 1st pleopod little curved, tapering from stout base to a long thin distal portion (compared to *E. aspinifera* n.sp., Fig. 10G, the thin terminal portion is very much longer); coloured brown-dark brown; males up to 3.4 mm, mature females 2.5-3.0 mm (Australian specimens).

REMARKS: The Australian specimens of *E. octagonalis* are smaller and tend to be more narrow than the holotype, which is the only specimen described from India. Kemp (1917) describes the carapace as slightly broader than long: measuring his figure of the holotype (Fig. 5) the carapace width to length ratio (excluding rostrum) is ca. 1.1. Some Australian specimens approach this ratio, in others the carapace length is greater. One other difference between the Australian specimens and Kemp's description is that the former have a subterminal tooth on the dactyli of the 1st walking legs (Fig. 6P), as well as on legs 2-4. Kemp (1917) states that in the holotype the dactylus of the 1st walking leg is "unarmed". Subterminal teeth on the dactyli of the 1st walking legs are often smaller than those on other legs and no other hymenosomatid is known in which teeth are only present on the dactyli of legs 2-4. It is possible that Kemp overlooked the subterminal teeth among the long setae on the dactyli of the 1st pair of walking legs.

The Australian specimens are considered to be conspecific with the holotype of *E. octagonalis* until examination of further Indian specimens shows a consistent difference in the shape of the carapace.

MATERIAL EXAMINED: QUEENSLAND: Victoria Pt., Moreton Bay, 12.ix.1962 and 11.x.1962, F. C. Vohra, 3 ov.♀♀, 3 im.♀♀, Stns 6 and 7 (QM W.2339, W.2344, W.2352, W.2354); South Dunwich, Moreton Bay, 15.vii.1962 and 12.viii.1962, F. C. Vohra, 3 im.♀♀, Stns 4 and 5 (QM W.2360; AM P.20181); Dunwich, Moreton Bay, 17.iv.1973 and 4.v.1973, J. S. Garth, 4♂♂, ♀, 3 im.♀♀, sandy mud flats with turnable rocks (with *Elamenopsis lineata*) (AHF JG 6-73, JG 9-73).

## **ELAMENOPSIS TORRENSICA** n.sp.

Figs. 4B, 6Q

TYPE LOCALITY AND TYPE: Thursday Island, Torres Strait, Queensland, Australia; HOLOTYPE: undated, ♀ (4.3 mm, all legs and chelipeds detached), Old Collection (AM P.20166).

DIAGNOSIS: Carapace approximately octagonal; lateral carapace walls without spines or crests; rostrum consisting of three rounded lobes which are narrow and separate, without fringing setae, lateral lobes well spaced from medial lobe, pointing slightly upward and curving slightly inward, medial lobe longest and pointing forward; walking legs not laterally compressed, dactyli with one subterminal tooth.

DESCRIPTION: Not including male features:— carapace width to length ratio 1.07 (Fig. 4B); dorsal carapace surface concave, with gastro-cardiac, cervical and thoracic grooves strongly indicated, carapace walls bulge laterally (not shown in Fig. 4B); anterior lateral carapace angles obtuse, midlateral carapace borders curve slightly in behind anterior lateral angles making them slightly prominent; posterior lateral angles obtuse, without spines; rostrum reaching beyond eyes; eyestalks short, corneas visible dorsally; postocular lobes developed into acute teeth; interantennular septum strong; a slight rostral keel on medial lobe; small acute antennal spines; exopodites of 3rd maxillipeds largely hidden; female chelipeds ca. 1½ X carapace width, fingers with small teeth; walking legs ca. 2 X carapace width, moderately stout, dactylus tapering uniformly, curved distally, with a subterminal tooth and a row of short setae ventrally (Fig. 6Q); female abdomen with segments 1 and 2 visible dorsally, a strong ridge across distal edge of segment 1, segment 5 of fused article (segments 3-5) appears to be very long and broad, constituting most of the abdomen, telson broad triangular; light setation on legs, mouthparts and lateral walls of carapace.

REMARKS: Although only a single female specimen has been found, it is clearly different from other *Elamenopsis* species and may confidently be described as a new species.

*E. torrensica, E. octagonalis* and *E. aspinifera* n.sp. are related to the *Elamenopsis* species with short tripartite rostra of narrow lobes and with unflattened legs, e.g. *E. woodmasoni, E. alcocki, E. exigua* and *E. introversa*. They differ from all except *E. introversa* in having the lobes unfused at the base, at least in dorsal view. *E. torrensica* is probably most closely related to *E. introversa*; these species may be distinguished by the narrower shape of the anterior of the carapace, very long legs and crests on the lateral carapace walls in *E. introversa*, as well as by less conspicuous features. *E. aspinifera* n.sp. is probably most closely related to *E. octagonalis*; it differs from *E. octagonalis* in carapace shape, male 1st pleopods and in the absence of teeth and spines in the usual places: postocular lobes, antennal spines, lateral carapace walls and dactyli of walking legs.

*E. torrensica, E. octagonalis* and *E. aspinifera* n.sp. have been collected in Australia from localities where marine salinities prevail, but where salinity is lowered in summer due to freshwater discharge from rivers.

The name *torrensica* (feminine) is based on the type locality of this species, Torres Strait.

MATERIAL EXAMINED: Holotype.

## **ELAMENOPSIS ASPINIFERA** n.sp.

Figs. 3I, 5G, 6R, 8D, 10G

TYPE LOCALITY AND TYPES: Weipa, Queensland, Australia; HOLOTYPE: July, 1972, W. McCormick, ♂ (3.1 mm, 1st pleopod detached and mounted on a slide, only one cheliped and four legs present, all detached), benthos off mangroves (QM W.4069); PARATYPE: Rooney's Bridge, Ross River, Townsville, Queensland, 13.ix.1969, J. S. Lucas, ♀ (3.0 mm, slightly damaged) ovigerous when collected, released larvae in laboratory (JCU).

DIAGNOSIS: Carapace subcircular, lateral carapace walls without spines; rostrum consisting of three separate spine-like lobes, fringed with short setae, lateral lobes well spaced from medial lobe and pointing slightly upward, medial lobe longest and pointing forward; walking legs not laterally compressed, dactyli without subterminal teeth; male 1st pleopod with thin terminal portion short and terminating bluntly.

DESCRIPTION: Carapace width to length ratio 1.00 (♀), 1.03 (♂); dorsal carapace surface concave, with cervical and thoracic grooves not as strongly defined as gastro-cardiac groove; anterior lateral angles very obtuse and hardly evident, posterior lateral angles rounded obtuse; rostrum outreaching eyes; eyestalks short; corneas visible dorsally; postocular lobes undeveloped; basal segment of antennules with a strong lateral tooth; flagellum of antennae very long, much longer than basal portion; interantennular septum strong, continuous with strong rostral keel from medial lobe of rostrum; no antennal spines; palp of 3rd maxillipeds long, about length of merus, exopodite largely concealed; length of male chelipeds ca. 2 X carapace width, merus setose anteriorly, carpus setose anteriorly and dorsally, propodus inflated, particularly expanded ventrally (Fig. 5G), fingers with three large teeth proximally and several smaller teeth distally; length of female chelipeds ca. 1½ X carapace width, with similar but smaller teeth on fingers; walking legs slender, length ca. 2 X carapace width, dactyli tapering to a long thin point, straight proximally, terminal point curving, with a row of short setae and scattered long setae on ventral and dorsal edges (Fig. 6R); female abdomen elongate oval, segments 1 and 2 visible dorsally, segment 2 and fused segments 3 and 4 very short, fused segment 5 elongate, constituting ca. ¾ of abdomen length, segment 5 set at ca. 90° to segments 2-4, abdomen broadest at segment 5, telson very broad triangular; male abdomen with segments 3-5 fused (Fig. 8D), segment 2 shorter than segment 1, fused article constituting ca. ⅔ abdomen length, telson triangular with convex sides, abdomen broadest at segment 1, narrower at segment 2, fused article expanding to equal breadth of segment 1 ca. ¼ along its length, then constricting abruptly to become narrower than segment 2, then tapering down to narrow telson, fused article with an obtuse point on each side at its maximum breadth; male 1st pleopods tapering strongly from stout base into narrow distal portion of uniform thickness (Fig. 10G), distal portion slightly curved toward abdomen, fine terminal portion angled toward sternum, with several rows of short setae distally; setation on legs, mouthparts, lateral walls of carapace and anterior surfaces of chelipeds; mature male and female 3.1 and 3.0 mm, respectively.

REMARKS: *E. aspinifera* is compared with other species of *Elamenopsis* in the Remarks on *E. torrensica*. The name *aspinifera* (not bearing spines; Latin, feminine) refers to the absence of spines on this species.

MATERIAL EXAMINED: Type material listed above.

## **HYMENICOIDES** Kemp, 1917

*Hymenicoides* Kemp, 1917:267 (type species, by original designation, *Hymenicoides carteri* Kemp, 1917).

DIAGNOSIS: Carapace subcircular, dorsal carapace surface concave, with well defined grooves; rostrum absent; eyes visible dorsally; epistome narrow, breadth ca. 2 X length; pterygostomial region plain; 3rd maxillipeds very narrow, ischium shorter than merus along lateral edge, palp elongate, dactylus especially elongate, reaching to posterior edge of mouth-frame; chelipeds much stouter than walking legs in males and females, very inflated in large males; walking legs moderately stout, length ca. 3 X carapace width, dactyli with a large subterminal tooth and small teeth; female abdomen without fused segments; male abdomen without fused segments, with a trilobate telson; male 1st pleopods strongly bent, with complex apex including long subterminal setae, semicircular lip and denticulate lobe.

SPECIES OF *HYMENICOIDES:* The genus is monospecific. *H. carteri* has been collected from two freshwater-brackish localities in the Gangetic Delta, West Bengal and Bangladesh. No specimens of *H. carteri* have been reported since Kemp (1917).

REMARKS: *H. carteri* occurs in the region of the greatest number of *Elamenopsis* species and in most features described by Kemp (1917) it appears to belong with the *Elamenopsis* species. Kemp did not describe the female reproductive structures and a finding of fused segments in the female abdomen, lack of pleopods, etc., would have confirmed the relationship with *Elamenopsis*. However, during a brief visit to the British Museum (Natural History) in 1975, I examined four cotypes and found that the male and female reproductive morphologies are quite different from the characteristic *Elamenopsis* pattern.

The female abdomen has normal segmentation and four pairs of pleopods. The sternal region is normal and the genital apertures are on small prominences. The female chelipeds are unusually large for a female hymenosomatid, as described by Kemp (1917). The male abdomen is without fused segments. It is unusually broad and contoured as figured by Kemp (1917) (Fig. 21 shows only whole segments 3-5 and telson). The trilobate telson results from contouring of its lateral regions to provide cavities to receive the apices of the 1st pleopods. The 1st pleopods are more complex than those described for any other hymenosomatid. Looking at the pleopods *in situ* against the sternum with the abdomen raised: each pleopod turns inward and down beyond the moderately stout base, then about two-thirds along its length it bends up, projecting away from the sternum so that the apex meets the inner surface of the telson, when it is in place. The inflated apex is complex, with semicircular lips terminally (like Fig. 58G of Melrose, 1975), a row of long subterminal setae on the medial surface and two lobes on the abdominal side, the largest of which is covered in a regular pattern of denticles. The denticulation and complexity of the pleopod apices is suggestive of the pleopods of *Hymenosoma* species.

Reproductive morphology gives no support for the suspected affinity of *H. carteri* with the *Elamenopsis* species and it appears to be rather isolated within the family Hymenosomatidae.

MATERIAL EXAMINED: Hughli R., Sibpur, Calcutta, (S. Kemp, Jan. 1917), 2♂♂, ov.♀, im.♀, cotypes (BM 1919.11.1.121-123).

## **HALIMENA** Melrose, 1975

*Halimena* Melrose, 1975:106 (type species, by original designation, *Halimena aotearoa* Melrose, 1975).

DIAGNOSIS: Carapace elongate suboval, dorsal carapace surface shallow convex, without well defined grooves, lateral carapace angles obtuse; rostrum spade-shaped, separated from dorsal carapace surface by a ridge, without a keel; epistome breadth almost 2 X depth; pterygostomial regions plain; 3rd maxillipeds broad, almost filling mouth-field, ischium longer than merus along lateral edge; walking legs slender, length ca. 2 X carapace width, dactyli with a single subterminal tooth; male and female abdomens without fused segments.

SPECIES OF *HALIMENA:* The genus is monospecific. *H. aotearoa* occurs in New Zealand.

REMARKS: This genus was established by Melrose (1975) for a rare species represented by four specimens. Only very small males have been seen. Melrose (1975) regards *Halimena* as being closely related to *Elamena* (especially to the "triangular" *Elamena* species), but differing from it in having the rostrum separated from the dorsal carapace surface and in having a short epistome. Details of the male 1st pleopods and larval morphology are desirable.

## **AMARINUS** n.gen.

TYPE SPECIES: *Elamena? lacustris* Chilton, 1882 is hereby nominated as the type species of the new genus. *A. lacustris* is the species of *Amarinus* n.gen. most widely distributed on different land masses, it has been well described and figured in the literature, and an undisputed holotype is extant, although it is an immature female specimen.

DIAGNOSIS: Carapace approximately circular to oval, with width greater than length; dorsal carapace surface flat or slightly concave, with well defined grooves; carapace angles obtuse and rounded, sometimes developed into small spines; rostrum separated,from dorsal carapace by a ridge or groove or both, rostrum spade-shaped and deflexed, concave laterally, base of rostrum extending laterally over eyestalks to meet postocular lobes; epistome short, width at least 2 X length; pterygostomial regions usually plain; 3rd maxillipeds broad, slightly separated medially, ischium subequal with or shorter than merus along lateral edge; chelipeds stouter than walking legs, particularly in large males, in which propodus is very deep; walking legs of moderate thickness, dactyli without teeth or with one tooth, dactyli little curved; abdomens on both sexes without fused segments; female abdomen oval; male abdomen narrow triangular, with intercalated plates laterally at base of telson, plates articulated or fused with telson and articulated with segment 5 (not described in *A. woltereckí*); male 1st pleopods stout, curved at base, otherwise with little curvature, terminal portion with fine setae in tufts or scattered, terminating in one or several lobes.

SPECIES OF *AMARINUS:* Based on Holthuis (1968) and Lucas (1970).

| **Species** | **Distribution** | **Habitat** |
|---|---|---|
| *A pilosus* (A. Milne Edwards, 1873) | New Caledonia | freshwater |
| *A. laevis* (Targioni Tozzetti, 1877) | southern Australia | brackish |
| *A. lacustris* (Chilton, 1882) | S.E. Australasia | freshwater |
| *A. woltereckí* (Balss, 1934) | Mindanao, Philippines | freshwater |
| *A. angelicus* (Holthuis, 1968) | Papua-New Guinea | freshwater |
| *A. paralacustris* (Lucas, 1970) | eastern Australia | brackish |
| *A. latinasus* n.sp. | N.E. Australia | brackish |

REMARKS: The *Amarinus* species have been assigned to various genera and recent authors have included them in the genus *Halicarcinus*. However, Holthuis (1968) questioned whether the four freshwater species were congeneric with *Halicarcinus planatus* (Fabricius), the type species of the genus *Halicarcinus* White; he noted their common features and suggested that they may belong together in another genus. Holthuis had access to insuffïcent hymenosomatid material to resolve the status of the freshwater species. It has been resolved by this study, and three related brackish water species are included with the four freshwater species in a new genus.

The geographical distributions of the freshwater *Amarinus* species are notable. In addition to the Australian mainland they have been reported from eight different islands scattered over 9,000 km of ocean: Mindanao, Papua-New Guinea, New Caledonia, Norfolk Island, Lord Howe Island, New Zealand, King Island and Tasmania. Their distribution suggests a widespread ancestral species which occurred through the region at times when these islands were variously interconnected by land-bridges. However, the land-bridges between most of these land masses were very ancient, much more ancient than the probable Tertiary – Recent origin of the hymenosomatids. There are no fossil records of the Hymenosomatidae (Glaessner, pers comm.) to illuminate their origins and previous distributions.

The *Amarinus* species form a distinctive homogeneous taxon. They all inhabit low salinity environments, they are all brown to dark brown and pubescent and most species are large relative to the typical hymenosomatid size. With *H. hodgkini* they are unique in having intercalated plates at the articulation of segment 5 and the telson of the male abdomen. Among Brachyura, only Dromiidae are also known to have this character (Holthuis, 1968). Other distinctive features are deflexed spade-shaped rostrum; dactyli of walking legs being relatively straight, without teeth or with a single inconspicuous tooth; and stout male 1st pleopods.

*Amarinus* is not closely related to the other genus with predominantly brackish and freshwater species, *Elamenopsis* (see Remarks on this genus). They are similar to the *Halicarcinus* species but differ in the basic rostral form (unilobe versus trilobe), type of male 1st pleopods and intercalated plates of the male abdomen. The presence of these plates in one species of *Hymenosoma* suggests an affinity between these genera and there are several other important features in common: basically unilobe rostrum, male 1st pleopods relatively straight and with a complex apex, and no fused abdominal segments. With the exception of the monospecific *Halimena* and *Neohymenicus* n.gen., they are the two genera in which the rostrum is basically a unilobe structure and separate from the dorsal carapace surface.

The name *Amarinus* (not marine; Latin, masculine) refers to the habitats of these species.

MATERIAL EXAMINED (other than Australian species): *Amarinus pilosus:* Oubatche, New Caledonia, Apr. 1898, C. Hedley, im.♀ (AM G.1833).

## **AMARINUS LAEVIS** (Targioni Tozzetti)

Figs. 4C, 7A, 10D

*Hymenosoma laeve* Targioni Tozzetti, 1877:179-82, pl. 11 figs. 3a-e (fig. 3d is incorrectly labelled 5d). — Tesch, 1918:28 ("species *incertae sedis*"). — Lucas, 1974:142; 1976:268. — Holthuis, 1975:133.

*Hymenosoma australe* Haswell, 1882b:754; 1882c:115, pl. 3 figs. 2, 2a. — Fulton and Grant, 1906b:19. — Montgomery, 1921:93-5.

*Halicarcinus laevis.* — Kemp, 1917:247.

*Hymenicus australis.* — Tesch, 1918:12-13.

*Halicarcinus australis.* — Hale, 1927:118, fig. 115. — Montgomery, 1931: 423-5, pl. 27 figs. 4, 4a. — Lucas, 1970:277; 1971:475-82, figs. 1-3 (larval morphology); 1974:142-3; 1976:268. — Griffin, 1972:65-6. — Holthuis 1975:133.

TYPE LOCALITY AND TYPES: Melbourne, Australia. The type specimens which were kept in the Museo Zoologico de "La Specola", Firenze, Italy, are not extant; they were lost during World War II (M. Poggesi, pers. comm.). There are two syntypes of *Hymenosoma australe* Haswell in the Australian Museum (see Griffin (1972) and Material Examined section for details; they are ♂ and ♀ specimens, not 2♀♀ as given by Griffin).

DISTRIBUTION: Temperate Australia in estuaries; from Moore River on the west coast to Brisbane River on the east coast. Snelling (1959) describes its distribution in the Brisbane River and Lucas and Hodgkin (1970a, b) describe the distribution of crab instars and larval stages in the Swan River.

DIAGNOSIS: Mature specimens rarely less than 10 mm; males and females up to 22 mm and 18 mm, respectively; antero-lateral carapace margins without a row of teeth or thin spines; antennal spines acute and prominent; male 1st pleopod not tapering at apex, apex complex, with several lobes and tufts of setae; propodus of chela very deep in large males, with knife-edge ventrally and large pulvinus (a sac arising between the bases of the fingers).

DESCRIPTION: The following is additional to the descriptions of Targioni Tozzetti (1877), Haswell (1882b, c) and Montgomery (1931), and details in the Diagnosis above:— posterior lateral carapace angle sometimes with an acute tooth; lateral borders of rostrum raised, terminating in spines which sometimes are very prominent to make apex of rostrum almost trifid; dactyli of walking legs with single tooth in first few crab instars, sometimes persisting in later instars; female abdomen convex and suboval, with two longitudinal grooves near midline, segments 1 and 2 short, of similar width, approximately half carapace width, segments 3-5 successively increasing in length and width, telson arcuate, longer than preceding segments, approximately 0.4 of whole abdomen length; intercalated plates of male abdomen fused with telson with inconspicuous sutures; body and legs covered with short setae, denser on body in mature females than mature males; coloration orange-brown to very dark brown, chelae of large males orange.

Targioni Tozzetti's Figure 3a of the dorsal carapace is misleading in the general shape of the carapace and rostrum, and over-sized eyes. The eyes are shown in normal proportion in Figure 3b (Targioni Tozzetti, 1877).

REMARKS: Between Targioni Tozzetti's description and this study only two authors referred to his name, *Hymenosoma laeve*. Kemp (1917) suggested that *Hymenosoma laeve* belonged in the genus *Halicarcinus* (he may have suspected that *Hymenosoma australe* Haswell was synonymous, because he does not mention *Hymenosoma australe*) and Tesch (1918) included *Hymenosoma laeve* with *Hymenosoma gaudichaudii* Guerin at the end of his hymenosomatid monograph in a section entitled "Species *incertae sedis*". Most authors were unaware of Targioni Tozzetti's description, for a few years later Haswell (1882b, c) described the taxon again and all later authors except Kemp (1917) used Haswell's specific name, often as *Halicarcinus australis*. Thus, although *Hymenosoma laeve* Targioni Tozzetti is the senior synonym for this taxon, it has remained unused in the primary zoological literature for more than fifty years and, according to I.C.Z.N. (1961) Article 23(b), it is to be considered a forgotten name *(nomen oblitum)*. The name *Hymenosoma laeve* Targioni Tozzetti was proposed for suppression under the plenary powers of the International Commission of Zoological Nomenclature (Lucas, 1974) and then withdrawn (Lucas, 1976) when Holthuis (1975) considered the proposal unnecessary.

*A. laevis* is the largest Australian hymenosomatid and mature specimens can be readily distinguished by their size from other Australian *Amarinus* species, with which it has sometimes been confused. Other features by which *A. laevis* may be readily distinguished from *A. lacustris* and *A. paralacustris* are its prominent and acute antennal spines, untapering 1st male pleopods and the prominent pulvinus which develops on the cheliped propodus of males at their pubertal/terminal moult (Lucas and Hodgkin, 1970a).

Throughout its distribution, *A. laevis* is quite constant in morphology, with minor variation in characters such as the degree of development of the teeth on the posterior lateral angles, degree of trifidness of the rostrum and number of tubercles on the merus of the male chelipeds.

MATERIAL EXAMINED: QUEENSLAND: Brisbane R., Chelmer, 7.x.1940, H. A. Longman, ov.♀ (AM W.1151); Mud Island, Moreton Bay, 27.vi.1941, V. F. Collin,♂ (QM W.1271); Brisbane R., Darra, 19.ii.1942, V. F. Collin, im.♀ (QM W.1473); Brisbane R., 14 miles from mouth, Dec. 1964, I.M.S.,♂, ♀ (JCU). NEW SOUTH WALES: Tweed River, 24.iv.1883, J. Steel, ov.♀, im.♀ (QM Mo.2984); Georges R., Picnic Point, 21.i.1967, J. S. Lucas, ♂, 2♀♀, *A. paralacustris* also collected here (AM P.20175); Budgewoi Lake, 7.ii.1965, J. S. Lucas, ♂ (AM P.20176); Stony Pt., The Broadwater, Myall Lake, 17.ix.1975,♂, im.♀ (AM). VICTORIA: Williamstown, Port Phillip, Victoria, undated,♂ (10.5 mm, dried, badly damaged by insects, right walking leg 1 and left walking legs 1 and 2 absent),♀ (12.2 mm, dried, slightly damaged by insects) Haswell Collection No. 210 (syntypes of *Hymenosoma australe* Haswell; both specimens are glued to a glass plate with a red spot and labels cut from Haswell, 1882c) (AM P.15398). Yarra R., 21.iii.1934, J. E. Dixon, 4♂♂, im.♀ (labelled *Halicarcinus lacustris,* J. Clarke) (NMV); Yarra R., Moonee Ponds, 30.i.1965, J. S. Lucas, 3♂♂,3im.♀♀(NMV). TASMANIA: Huon, Meredith, Arthur, Pieman and Liven Rivers, Egg Island and Grant's Lagoon, various dates 17.v.1963 — 28.vii.1964, B. C. Mollison, 39♂♂, 8 ov.♀♀, 9♀♀, 2 im.♀♀ (in eight containers) (IFCT); Derwent R., Lime Kilns, 15.ix.1963, 23♂♂, 24 im.♀♀, seven unidentifiable individuals (labelled "from 2½ lb brown trout (DS9 tag)"; most crabs are intact except for some legs missing; the smallest crab is 2.9 mm and the largest male and female are 7.3 mm and 5.7 mm respectively; there is little else in the stomach contents apart from some plant material and fish vertebrae) (IFCT). WESTERN AUSTRALIA: Swan R., Barkers Bridge, 8.i.1964, J. S. Lucas, 4♂♂, ov.♀, 3 im.♀♀ (WAM); Moore R., Nov. 1964, C. Prince, 3♂♂, 3 ov.♀♀ (WAM).

## **AMARINUS LACUSTRIS** (Chilton)

Figs. 4D, 7B, 10E

*Elamena ? lacustris* Chilton, 1882:172.

*Hymenosoma lacustris.*— Chilton, 1883:69, pl. 1 fig. 2a-e.— Fulton and Grant, 1902:59-61, pl. 8.— Chilton 1915:316-20, fig. 1; 1919:93-5.

*Halicarcinus lacustris.*— Kemp, 1917:247.— Holthuis, 1968:111-12.— Walker, 1969:163-5.— Lucas, 1970:267-77, figs. 3a, 3d, 4.— Lucas, 1971:428, fig. 5I (embryo).— Melrose, 1975:84-8, figs. 41, 42.

*Hymenicus lacustris.*— Tesch, 1918:12.

See Holthuis (1968) and Melrose (1975) for further Synonymy.

TYPE LOCALITY AND TYPES: Lake Pupuke (= Lake Takapuna), Auckland, New Zealand; HOLOTYPE: im.♀ (labelled *Hymenosoma lacustris,* Chilton 1882; no details of collector or date of collection) (Canterbury Museum AQ 3287).

DISTRIBUTION: South-eastern Australasia. Lakes and streams in Victoria, South Australia, Tasmania, King, Norfolk and Lord Howe Islands, and North Island, New Zealand. Found in salinities 0.1-9.6°/oo and most commonly within the range 1-6°/oo in Victoria, Australia (Walker, 1969).

DIAGNOSIS: Rarely exceeding 10 mm carapace width; antero-lateral carapace margins without a row of teeth or thin spines; rostrum not fused with postocular lobes in a broad band; orbits extending dorsally to meet carapace rim; antennal spines obtuse and inconspicuous; female genital apertures 0.6-0.8 mm wide, without a medial prominence; eggs 0.65-0.8 mm diameter; mean value of breadth/length ratios of inner rami of female pleopods ca. 0.25; telson length/total abdomen length ca. 0.25 in mature females; male 1st pleopod very stout, tapering to a simple tip.

DESCRIPTION: Melrose (1975) gave a full description of this species from New Zealand and Norfolk Island specimens. However, she did not describe the female reproductive structures and eggs (see Diagnosis), which are important in distinguishing *A. lacustris* from its sibling species, *A. paralacustris,* in Australia.

Comparing *A. lacustris* specimens from Australia and Tasmania with Melrose's descriptions of New Zealand and Norfolk Island specimens, some minor consistent differences were found (Table 2).

TABLE 2. Minor differences between *Amarinus lacustris* specimens from New Zealand and Norfolk Island (described by Melrose, 1975) and those from Australia and Tasmania.

| | **New Zealand and Norfolk Island** | **Australia and Tasmania** |
|---|---|---|
| rostral keel: | absent | a small ridge |
| large ramus of antennule: | 2 segments | 3 segments |
| basal tooth of dactylus of ♂ chela: | rarely present | well developed |
| dactyli of walking legs: | sometimes remnants of dentition | 1 small tooth in specimens less than 5 mm |
| male abdomen | | |
| (a) telson: | shorter than 3rd segment, semi-circular | equal to 3rd segment, triangular with rounded apex. |
| (b) width 3rd segment/ width 1st segment: | 0.55 | 0.50 |

REMARKS: The populations of *A. lacustris* on six land masses separated by many hundreds of miles of ocean are genetically isolated, since this species only occurs in inland low salinity waters and has no free larval stages (Lucas, 1970). Morphological differences between specimens from Victoria, Tasmania, New Zealand and Norfolk Island have been described by Fulton and Grant (1902) and Chilton (1919). The differences that they observed relate to: carapace shape, size of teeth on the carapace angles, angle and shape of the rostrum, dentition and tuberculation of the male chelipeds, shapes of male abdominal segments, shape of 3rd maxillipeds, and general body hairiness. These authors acknowledged that there was considerable variation among specimens from one locality and they were not prepared to give separate taxonomic status to the isolated populations. Some of the differences which they observed are in characters which vary with age, e.g. carapace shape, male chelipeds and hairiness, and in other characters there is as much variation between specimens from different Australian-mainland localities as between specimens from Victoria and Tasmania or New Zealand. The only consistent differences found so far between specimens from either side of the Tasman Sea are those shown in Table 2, and it is not proposed to establish specific or subspecific taxa on the basis of these minor differences.

*A. lacustris* is morphologically very similar to *A. paralacustris,* a brackish water species occurring along the eastern Australian mainland. The only significant differences between crab instars of these species are differences in the female reproductive apparatus which are related to the different sizes and numbers of eggs produced. *A. lacustris* has no free larval stages and ovigerous females carry a small number of large yolky eggs, while *A. paralacustris* has normal larval development and its eggs are half the diameter of those of *A. lacustris* and much more numerous (Lucas, 1970). Thus the female genital apertures are broader in *A. lacustris* and the inner rami of the pleopods (which bear the eggs) are narrower in *A. lacustris* than in *A. paralacustris.* Using morphology, mature females and late instar immature females are the only crabs instars which can always be identified to species. Some large males and immature females from Australian localities can be identified as *A. lacustris* by the absence of teeth on the dactyli of walking legs: the tooth on the dactylus of each walking leg becomes proportionally smaller in larger instars and in *A. lacustris* specimens of greater than 5 mm carapace width it is usually absent, while it is always present in *A. paralacustris.*

The male pleopods of these species are very similar and cannot be reliably distinguished (Figs. 10A, 10E).

In those characters in which there are consistent differences between *A. lacustris* specimens from Australia and New Zealand-Norfolk Island (Table 2), *A. paralacustris* is like the Australian specimens.

The problematical distribution of *A. lacustris* on six isolated land masses, and its degree of genetic compatibility with *A. paralacustris,* which only occurs on the Australian mainland, were discussed by Walker (1969) and Lucas (1970). Both consider that the available evidence is only compatible with a recent origin of *A. lacustris* in Australia and subsequent dispersal to Norfolk and Lord Howe Islands and New Zealand. Walker (1969) suggested rafting on floating debris in the East Australian Current and Lucas (1970) suggested aerial transport among the feathers or on the feet of water fowl, which fly across the Tasman Sea, as the method of dispersal. Whatever the explanation for the origins of these isolated populations, it would seem to be quite unique, as there is no other macroscopic freshwater invertebrate which also occurs on all the above land masses.

MATERIAL EXAMINED: VICTORIA: Lake Colac, 11.i.1967, K. Walker and J. S. Lucas, 20♂♂, 3 ov.♀♀, 3 im.♀♀ (AM P.20173); Skeleton Creek, Apr. 1967, K. Walker, 12♂♂, 2♀♀, 6 im.♀♀ (NMV). TASMANIA: Templestone Lagoon, Orielton Lagoon, Rebecca Lagoon, Old Mines Lagoon, 8.v.—21.x.1963, B. C. Mollison, 14♂♂, 5 ov.♀♀, 15 im.♀♀ (IFCT); King Island, Bass Strait, undated, ♂ (NMV). SOUTH AUSTRALIA: Finnis R., Finnis, 23.i.1965, J. S. Lucas, 5♂♂, 2 ov.♀♀, chlorinity 0.6°/oo (SAM C.19741); Pt. Sturt, Lake Alexandrina, 23. i. 1965, J. S. Lucas, 10♂♂ ov.♀, 9 im.♀♀, 2 juvs., under rocks, 0.4°/oo chlorinity (SAM C. 19743); Eight-mile Creek, Cape Northumberland, undated, ♂ (SAM). Localities not in Australia (only eggs of ovigerous females examined). NEW ZEALAND: Lake Pupuke, Auckland, undated, 2 ov.♀♀ (from Dr C. Chilton collection, presented Fulton and Grant, June 1902) (NMV). LORD HOWE ISLAND: Apr. 1933, A. A. Livingstone, 5 ov.♀♀, freshwater stream (AM P.10344).

## **AMARINUS PARALACUSTRIS** (Lucas)

Figs. 4E, 7C, 10A

*Halicarcinus paralacustris* Lucas, 1970:275-7, figs. 3c, e; 1971:475-82, figs. 3JK, 5E-H (larval morphology).

TYPE LOCALITY AND TYPES: Cook's River, near Campsie, N.S.W. HOLOTYPE: ov.♀ (6.5 mm) 19.ii.1965, J. S. Lucas, among detritus in littoral zone, 7.4°/oo Cl. (AM P.15943). PARATYPES: 36 specimens, collection details as for the holotype, lodged in the following musems: 4♂♂, 2 ov.♀♀, 7 im.♀♀ (AM P.15944 and P.15945); 4♂♂, ov.♀, 6 im.♀♀ (NMV); 3♂♂, ov.♀, 7 im.♀♀ (QM W.3023); ov.♀ (JCU).

DISTRIBUTION: Eastern Australian mainland, in estuaries along the coast from Anglesea, Victoria, to Russell R., North Queensland.

DIAGNOSIS: Rarely exceeding 10 mm carapace width; antero-lateral carapace margins without a row of teeth or thin spines; rostrum not fused with postocular lobes in a broad band; orbits extending dorsally to meet carapace rim; antennal spines obtuse and inconspicuous; female genital apertures 0.4-0.5 mm wide, generally with a curved medial prominence; eggs less than 0.4 mm diameter; mean value of breadth/length ratios of inner rami of pleopods ca. 0.4; telson length/total abdomen length ca. 0.35 in mature females; male 1st pleopods very stout, tapering to a simple tip.

DESCRIPTION: Lucas (1970) gave a description of this species based on specimens from the southern temperate part of its distribution. However, specimens of *A. paralacustris* from tropical North Queensland differ from the southern specimens in the following features:— thoracic grooves on dorsal carapace surface angled more laterally; with three prominent lobes in pterygostomial region (less developed in small specimens); male 1st pleopods with more elongate pointed apex which projects away from abdomen; female genital apertures without medial prominences; eggs larger, approximating more to 0.4 mm than to 0.35 mm diameter.

REMARKS: This species is morphologically very similar to *A. lacustris* and to an extent genetically compatible with it (see Remarks on *A. lacustris*).

*A. laevis* occurs at all the temperate localities where *A. paralacustris* has been collected, but these brackish water species may be readily distinguished in their crab instars (see Remarks on *A. laevis*) and larval stages (Lucas, 1971).

On the basis of the temperature tolerances of their larvae, Lucas (1972) predicted that *A. paralacustris* would occur further north than *A. laevis* in the presence of suitable habitats. (At that time, the Brisbane River was the most northern locality reported for both species.) The prediction has been confirmed with the recent collection of *A. paralacustris,* but not *A. laevis,* in North Queensland. However, the North Queensland specimens differ from the southern specimens in several important features, including male 1st pleopod. Development of pterygostomial lobes in the northern specimens is unusual since these lobes are generally insignificant in *Amarinus* species. Further study of crab and larval morphology of specimens from various Queensland localities may indicate some separate taxonomic status for the North Queensland specimens.

MATERIAL EXAMINED: QUEENSLAND: Russell, North Johnstone, South Johnstone and Herbert Rivers, 11.xi.1975 — 28.xi.1976, R. G. Pearson, 12♂♂, 4 ov. ♀♀, 3 im. ♀♀, dredge, net, artificial substrate collector and sand wash samples (JCU). NEW SOUTH WALES: Violet Hill, Myall Lakes, 1975, ♂, 2 ov. ♀♀(AM).

### **AMARINUS LATINASUS** n.sp.

Figs. 4F, 6G, 7D, 10F

TYPE LOCALITY AND TYPES: Johnstone River, Queensland, Australia. HOLOTYPE: 30.xi.1972, M. Draper, ♂ (1.96 mm, with abdomen and 1st pleopod detached and mounted on a slide), among *Elodea* at low salinity (QM W.4066); PARATYPES: collection details as for holotype, 3♂♂(1.52, 1.72, 1.88 mm) (QM W. 4066); Weipa, Queensland, July 1972, W. McCormick, ov. ♀ (4.1 mm, 6 walking legs and left cheliped present, all detached), benthic zone in front of mangroves (QM W.4065).

DISTRIBUTION: Queensland, Australia (two known localities).

DIAGNOSIS: Rostrum broad, only slightly deflexed, abruptly tapering to a point; postocular lobes prominent in dorsal view, extending laterally along antero-lateral carapace borders, forming a shield with rostrum across anterior of carapace; dorsal carapace surface with only gastro-cardiac, cervical and thoracic grooves; dactyli of walking legs with a recurved tooth subterminally; female mature at less than 5 mm.

DESCRIPTION: The four male types are less than half the carapace width of the mature female paratype and their appearance is of immature specimens. Thus the description does not include characters of large males, such as cheliped size:— carapace subcircular (Fig. 4F), carapace width to length ratio 0.88-0.96; dorsal carapace surface flat in branchial regions, with convex cardiac region and less convex gastric region; lateral carapace walls vertical; anterior lateral carapace angles located well forward, rounded and very obtuse, posterior lateral angles not evident, with a small, acute spine below carapace rim in region of posterior lateral angle (not seen in female); eyestalks very short; postocular lobes prominent, continuous with rostrum; interantennal septum well developed; no rostral keel; no antennal spines; epistome width greater than 2 X length; pterygostomial region plain; Milne Edwards apertures oriented well anterior to cheliped bases; mouth-field wider than long; 3rd maxillipeds very broad, meeting medially, ischium shorter than merus along lateral edge, palp arising from inner surface of merus; exopodite hardly visible; female chelipeds slightly longer than carapace width, propodus stouter than walking legs, fingers slightly less than half total propodus length, cutting edges plain; walking legs ca. 1½ X carapace width, moderate thickness, dactyli little curved, with long setae along ventral edge; female abdomen oval, segments 1-5 progressively longer and broader, telson triangular with rounded apex, telson ca. ⅓ total abdomen length; eggs 0.3 mm diameter; male abdomen elongate triangular (Fig 7D), segments 1-5 subequal in length, segments 2-5 becoming progressively narrower, telson spade-shaped with broad apex; male 1st pleopod stout and straight (Fig. 10F), tapering slightly along its length, then tapering more abruptly to a pointed lobe terminally, with tufts of setae subterminally; coloured dark brown; scattered setae on legs and carapace walls, setae lining Milne Edwards apertures and dactyli of walking legs.

REMARKS: *A. latinasus* is the smallest of the *Amarinus* species. It is also distinguished from other *Amarinus* species by the large development of postocular lobes. There is some fusion between the rostrum and postocular lobes, but this is not as great as in *A. angelicus*; and while the fusion of rostrum and postocular lobes is in the horizontal plane in *A. latinasus,* it is in the vertical plane in *A. angelicus* and not visible in dorsal view.

In other characters in which the *Amarinus* species vary, e.g. carapace grooves, dactyli of walking legs, antennal spines, breadth of carapace and male 1st pleopods, *A. latinasus* is most like *A. lacustris* and *A. paralacustris.* The male 1st pleopod is similar to that of *A. angelicus,* but it is of the same form, i.e. terminating in a single lobe, as those of *A. lacustris* and *A. paralacustris.* The male 1st pleopd figured (Fig. 10F) is probably an immature form; the mature pleopod will show the same basic structure, but be more elongate.

The two localities where *A. latinasus* has been collected are at the opposite extremes of estuarine systems: in prevailing marine salinities at Weipa and in prevailing freshwater salinities at Johnstone River. Thus it is presumed to be a euryhaline brackish-water species. There are two other brackish-water *Amarinus* species, *A. laevis* and *A. paralacustris,* which occur in southern and eastern Australia, respectively. Thus, since it is probable that *A. latinasus* has a wider distribution in northern Australia than represented here (the region is very poorly collected), there may be at least one *Amarinus* species in most Australian estuaries.

The name *latinasus* (wide nose; Latin, masculine) refers to the broad rostrum of this species.

MATERIAL EXAMINED: Type material listed above.

## **HALICARCINIDES** n.gen.

TYPE SPECIES: *Halicarcinus nuytsi* Hale, 1927 is hereby nominated as type species of the new genus.

DIAGNOSIS: Carapace subcircular, dorsal carapace surface with sharply defined grooves; rostrum absent; eyes completely concealed in dorsal view by carapace; epistome broad, but breadth less than 2 X length; 3rd maxilliped broad, almost filling mouth-field, ischium shorter than merus along lateral edge, palp reaching only to junction of ischium and merus; walking legs ca. 2 X carapace width, dactyli without a row of teeth; chelipeds stouter than walking legs, especially in large males; female abdomen without fused segments; male abdomen narrow, with segments 3 and 4 fused (?); male 1st pleopods strongly curved, with stout base and thin distal portion.

SPECIES OF *HALICARCINIDES*: The genus is monospecific. *H. nuytsi* occurs in southern Australia.

REMARKS: This new genus is established for *H. nuytsi,* an unusual and rare species which was previously included in the genus *Halicarcinus* by Hale (1927, 1928). *Halicarcinides* is most closely related to *Halicarcinus,* but *H. nuytsi* differs conspicuously from the *Halicarcinus* species in having no rostrum and having the anterior carapace completely concealing the eyes in dorsal view. Some other differences from most *Halicarcinus* species are:— the epistome is longer, there are no rows of teeth on the dactyli of walking legs and, possibly, there are fused segments in the male abdomen. The uncertainty of this last character is because only one small male was examined during this study. Although it appeared to show segments 3 and 4 fused with a suture evident, Hale (1928), who examined a small series of both sexes, specifically stated that *H. nuytsi* has no fused segments in the male abdomen. Abdominal segments and sutures are sometimes inconspicuous in small male specimens and more specimens are needed to clarify the condition.

Another hymenosomatid species has no rostrum. This is *Hymenicoides carteri* Kemp, which has few other important characters in common with *Halicarcinides nuytsi*, and they are not closely related.

The name *Halicarcinides* (Greek, feminine) refers to the affinity with *Halicarcinus*.

### **HALICARCINIDES NUYTSI** (Hale)

Figs. 2F, 6I, 8C, 9D

*Halicarcinus nuytsi* Hale, 1927:118, fig. 116; 1928:98-9, fig. 22.

TYPE LOCALITY AND TYPE: St. Francis Island, South Australia; HOLOTYPE: undated, J. Verco, ov. ♀ (5.8 mm, dried specimen, some legs detached and damaged) dredged (SAM C1497).

DISTRIBUTION: Southeastern Australian mainland (3 localities).

DIAGNOSIS: Dorsal carapace rim lined with tubercles extending back to posterior lateral angles, tubercles most prominent near eyes.

DESCRIPTION: The following is additional to the descriptions of Hale (1927, 1928) and the Diagnosis:— portion of carapace over-reaching eyes with three short longitudinal ridges, one ridge above each eye and a slight medial ridge; postocular lobes and antennal spines absent; interantennular septum thin and elongate; dactyli of walking legs with a small sub-terminal tooth (Fig. 6I); female abdomen ovoid, segments 1-5 progressively longer and broader, telson arcuate, longer than preceding segments, approximately ⅓ total length of abdomen; eggs ca. 0.33 mm diameter; male abdomen widest at segments 3 and 4, suture (?) between segments 3 and 4, segment 5 with concave sides, telson triangular (Fig. 8C); male 1st pleopod bent at ca. 90° above base, distal portion relatively straight, terminal portion tapering to a point (Fig. 9D); largest male ca. 7 mm, mature females 4.9-5.8 mm.

REMARKS: It is most unusual that no specimens of *H. nuytsi* have been collected since 1930. In addition to the holotype from South Australia, a few specimens were collected from under rocks in the littoral zone at Long Reef, Collaroy, and Bottle and Glass Rocks, Port Jackson, N.S.W., all except one by Mr Melbourne Ward. Some of Ward's specimens were forwarded to Hale at the South Australian Museum (described by Hale, 1928) and have been lost, and four specimens are in the Australian Museum. The two localities in New South Wales were visited in 1965 to try to find more specimens, but only *Halicarcinus ovatus* was collected.

MATERIAL EXAMINED: NEW SOUTH WALES: Bottle and Glass Rocks, Port Jackson, 25.v.1926, M. Ward, ♀, between tide marks (AM P.9227); Long Reef, Collaroy, Mar. 1928 and Mar. 1929, M. Ward, ♂, ov. ♀ (AM P.9364 and P.9074); Long Reef, Collaroy, Jan. 1930, F. A. McNeill, im. ♀ (AM P.9432). SOUTH AUSTRALIA: Holotype.

## **NEOHYMENICUS** n.gen.

TYPE SPECIES: *Hymenicus pubescens* Dana, 1851 is hereby designated type species of the new genus.

DIAGNOSIS: Carapace subcircular, dorsal carapace surface with well defined grooves, lateral carapace angles obscure; rostrum triangular, deflexed, separated from dorsal carapace surface by a groove; epistome short, breadth ca. 2 X depth; pterygostomial region plain; mouth-field almost completely filled by 3rd maxillipeds, ischium subequal in length with merus along lateral edge; chelipeds stouter than walking legs, especially in large males, but not greatly inflated; walking legs moderately stout, dactyli with a subterminal tooth; male and female abdomens without fused segments; male 1st pleopods sickle-shaped, with stout base and thinner, strongly-curved distal portion, with a row of long setae subterminally.

SPECIES OF *NEOHYMENICUS:* The genus is monospecific. *N. pubescens* occurs in New Zealand.

REMARKS: Dana (1852) distinguished *Hymenicus* from *Halicarcinus* on the basis of the rostrum which is a "simple rounded or trilobate prominence", compared to "three teeth of *Halicarcinus*" and the walking legs which are "much longer and more slender than in any of the species of *Halicarcinus*". The new genus included four species: *Hymenicus pubescens, H. varius, H. novi-zealandiae* (synonymous with *H. varius* Dana, 1851 (Melrose, 1975)) and *Hymenosoma depressum* (excluded from the genus by later authors).

*Hymenicus varius* Dana should clearly be included in the genus *Halicarcinus.* Its rostral condition is variable and terminally trilobate in some specimens. It is very similar to *Halicarcinus cookii* and *H. ovatus* with which it has been confused (Melrose, 1975). *Hymenicus pubescens* Dana does not as readily belong in the genus *Halicarcinus.* Its rostrum is similar to that of *Halicarcinus bedfordi* and may be interpreted as fused trilobate, but it is also similar to the unilobe rostrum of *Hymenosoma* species. The arrangement of grooves on the dorsal carapace surface is unusual: in addition to the gastro-cardiac groove, the cervical and other anterior grooves are well defined, strongly outlining the gastric region (Melrose, 1975, Fig. 36), while the cardiac region of the carapace is hardly indicated. The dactyli of the walking legs have a single tooth and the male 1st pleopod has a subterminal row of long setae and is like that of an *Elamena* species. In fact, *Hymenicus pubescens* could equally well be a *Amarinus* species as a *Halicarcinus* species. It generally conforms with the diagnostic features of *Amarinus,* only the rostrum is more triangular than spade-shaped, the dorsal carapace grooves and male 1st pleopod are unlike *Amarinus* species (and unlike *Halicarcinus* species) and it has no intercalated plates in the male abdomen.

Larval morphology provides the most conclusive evidence that *Hymenicus pubescens* does not belong in the genus *Halicarcinus* or *Amarinus*. The zoeal stages show the lateral expansions of the 5th abdominal segment characteristic of *Elamena* zoeae. But, unlike the globular zoeae of *Elamena* species, the zoeae of *H. pubescens* have well developed dorsal and lateral spines (Wear, 1968). In crab and larval morphology, *Hymenicus pubescens* shows affinities with *Elamena, Halicarcinus* and *Amarinus,* but it belongs in a separate genus.

This conclusion regarding *Hymenicus pubescens* differs from Melrose (1975), who included it in the genus *Halicarcinus,* with *Hymenicus varius;* although recognising the unusual features of *H. pubescens.* Melrose's conclusion is at least partly explained by the fact that she included species now removed to *Amarinus* in the genus *Halicarcinus*, which was thus a more heterogeneous taxon.

With the inclusion of *Hymenicus varius*, type species of *Hymenicus* Dana by subsequent designation of Kemp (1917:246), in the genus *Halicarcinus* White, *Hymenicus* Dana becomes a junior synonym of *Halicarcinus* White and a new generic name is created for *Hymenicus pubescens* in this study.

*Hymenicus pubescens* Dana, 1851 should not be confused with *Halicarcinus pubescens* Dana, 1851, which is regarded as a probable synonym of *Halicarcinus planatus* (Rathbun, 1925; Garth, 1958). Melrose (1975) resolved the state of homonymy between the two species when *Hymenicus pubescens* was included in the genus *Halicarcinus* by rejecting the name *pubescens* Dana 1851, as published in combination with *Halicarcinus pubescens*, and proposing a replacement name *Halicarcinus patagoniensis* Melrose, 1975.

MATERIAL EXAMINED: NEW ZEALAND: 17 and 18.i.1964, J. S. Garth, 9♂♂, 12 ov.♀♀,♀, 2 juvs. (AHF); Parekura Bay, Bay of Islands, North Island, 10-12.ii.1973, J. S. Garth, 5 im. ♀♀, rocky outcrops on either side of gravel beach (AHF JG2-73).

## PART B, REVIEW OF BIOLOGICAL DATA

### LIFE CYCLES AND GROWTH

The hymenosomatids with free larval stages hatch from eggs 0.25-0.45 mm diameter and pass through three planktonic zoeal stages. The third zoeal stage moults to the first crab instar which settles from the plankton; there is no transitional megalopa larva. The first instar crab is small: carapace widths of *Hymenosoma orbiculare*, *Amarinus paralacustris*, *A. laevis* and *Halicarcinus planatus* are 0.9, 0.75, 1.0 and 0.95 mm respectively (Broekhuysen, 1955; Lucas, 1968; Boschi et al., 1969). There follows a series of crab instars which are not markedly different except in size and in relative proportions of features which show allometric growth, such as carapace width to length ratio. Differentiation of secondary sex characters occurs at an early stage and sex may be distinguished by abdomen shape at about the fourth crab instar. At an earlier stage than this, in *Halicarcinus planatus*, appropriate pleopods are present in males at the second crab instar (Richer de Forges, 1977).

After a series of immature crab instars there is a pubertal moult which is distinguished by morphological changes that are generally characteristic of Brachyura at this moult (Hartnoll, 1974). The female abdomen expands laterally and anteriorly and becomes more convex; the pleopods broaden and become more setaceous. The genital apertures and branchiosternal canals enlarge, but these are essentially in the mature form in late prepubertal instars. The change in abdomen size from immature to mature condition is particularly pronounced in hymenosomatid females. In *Amarinus laevis* and *Halicarcinus planatus*, the only hymenosomatids subjected to morphometric studies, the female chelae decrease slightly at the pubertal moult relative to body size (Lucas and Hodgkin, 1970a; fig. 8; Richer de Forges, 1977; fig. 10). At the pubertal moult in males the chelae increase in relative size (*Trigonoplax* species may be exceptional). In *A. laevis* males the chelae also develop a prominent sac (pulvinus) between the fingers. There may also be relative increases in cheliped length, rostrum size, body spine sizes and general setation in males at their pubertal moult; but the abdomen and male pleopods show little relative change, being essentially in their mature form in late prepubertal instars.

In crabs reared from eggs in the laboratory, Lucas (1968) found eight prepubertal crab instars for females of *Amarinus lacustris* and 10 to 12 or 13 for *A. paralacustris*. Size after the pubertal moult was 4.9-5.9 mm and 4.2-5.9 mm, respectively. Based on crabs maintained in an aquarium after collection in the field, Richer de Forges (1977) estimated that there were 11 prepubertal crab instars in the development of *Halicarcinus planatus* which reached approximately 14 mm at its pubertal moult. These are large numbers of instars considering the small mature sizes of these crabs. For comparison, *Scylla serrata* Forskål (Portunidae) reared in captivity reached 45.0-57.3 mm at its twelfth crab instar (Ong, 1966) and Hiatt (1948) estimated that *Pachygrapsus crassipes* Randall (Grapsidae) was 22 mm at its twelfth crab instar. Part of this size difference results from proportionally smaller growth increments in hymenosomatids; part is due to the smallness of first crab instars of hymenosomatids, a consequence of their small eggs and few larval stages. First instar crabs of *S. serrata* and *P. crassipes* are approximately 3.4 mm carapace width, which is larger than the adults of some hymenosomatid species.

In hymenosomatids, as in other Brachyura, intermoult periods increase as the crabs get older and larger. At the same time, percentage increments in carapace width, or other linear dimensions, decrease through the series of ecdyses. These trends have been shown for *Hymenosoma orbiculare* (cf. Broekhuysen, 1955), *Amarinus lacustris* and *A. paralacustris* (cf. Lucas, 1968), and *Halicarcinus planatus* (cf. Richer de Forges, 1977) in groups of crabs kept in the laboratory. *A. lacustris* and *A. paralacustris* took a minimum of 177 and 121 days, respectively, from hatching to pubertal moult when reared at 20 ± 1°C (Lucas, 1968). In field populations of *A. laevis* in the Swan River estuary, Western Australia, recruits which hatched in November-December reached 10-12 mm carapace width about five months later in April; at which time some females underwent their pubertal moult (Lucas and Hodgkin, 1970a). Water temperature was 21-27°C during this period. In contrast, the subantarctic hymenosomatid, *Halicarcinus planatus*, living in water temperature 1.5-8°C at Kerguelen Island, was estimated to take more than two years from hatching to its pubertal moult (Richer de Forges, 1977; fig. 17b). *H. planatus* occurs in atypically cold water; all other hymenosomatids are temperate or tropical, and the periods of immaturity of the *Amarinus* species are probably more typical.

There is a major division of hymenosomatid life cycles according to whether the pubertal moult is also the terminal moult. Crabs of the genera *Amarinus* and *Halicarcinus* have a common pubertal/terminal moult. Mature specimens of *A. lacustris* and *A. paralacustris* were kept for more than a year and mature specimens of *A. laevis, H. ovatus* and *H. rostratus* for some months without moulting. Indirect evidence from the field (suggested by Hartnoll, 1965) supports this laboratory observation: in these species there is no limb bud formation in mature crabs where pereiopods are lost. Richer de Forges (1977) also found a pubertal/terminal moult in *Halicarcinus planatus*. In contrast to these species of *Amarinus* and *Halicarcinus*, *Hymenosoma orbiculare* and *Elamenopsis lineata* females continue moulting after their pubertal moult (Broekhuysen, 1955; Lucas, unpubl. data).

There are no precise data for longevity of hymenosomatids in the field. In the laboratory some individuals of *Amarinus lacustris* and *A. paralacustris* survived for more than two years from hatching (Lucas, 1968), but this does not necessarily reflect longevity in the field. In population studies of three hymenosomatid species in non-marine habitats, *Hymenosoma orbiculare, Amarinus lacustris* and *A. laevis*, there was basically a one-year life cycle (Broekhuysen, 1955; Walker, 1969; Lucas and Hodgkin, 1970a). In size-frequency plots the mode of mature crabs virtually disappeared after the annual period of highest proportions of mature females, and predominantly small immature crabs remained. For *A. laevis* in the Swan estuary, Western Australia, the adult mortality occurred in mid-summer; but a few mature crabs survived to a second summer, as evidenced by a small proportion of individuals with very encrusted carapaces among the newly mature crabs in early summer. (Because these crabs do not moult after their pubertal moult, their cuticles become progressively encrusted with epiflora and epifauna.) Because of its long period of immaturity, *Halicarcinus planatus* lives longer than the species discussed above. Richer de Forges (1977) estimated the duration of its final instar as approximately 10 months, giving a total life-span of more than three years in Kerguelen Island populations.

## REPRODUCTION

Ovary development before the pubertal moult has been found in some hymenosomatid females. This was observed through the translucent carapaces of laboratory-reared *Amarinus lacustris* and *A. paralacustris* and confirmed by extrusion of an egg mass within two days of their pubertal moult (Lucas, 1968). *Halicarcinus ovatus* females also extrude eggs within two days of their pubertal moult (Lucas, 1968). Broekhuysen (1955) found well developed ovaries in an immature female of *Hymenosoma orbiculare*. Some hymenosomatid females may copulate before their pubertal moult: this was observed in laboratory populations of *Halicarcinus planatus* (Richer de Forges, 1977). Also, four of seven immature females of *Amarinus lacustris*, collected from the field, had spermatozoa in their spermathecae (Lucas, 1970). Copulation of immature females is physically possible because their genital apertures are essentially in the mature condition. However, among Brachyura it is exceptional for females to copulate prior to their pubertal moult (Hartnoll, 1969); parasitic pinnotherids are the only general exception to this pattern described so far.

The pubertal moult in male hymenosomatids is equivalent to the pubertal moult in females in terms of abrupt acquisition of mature features and it is appropriate to apply this name to the distinctive moult in the male. However, males of at least some species are sexually mature before their pubertal moult. Laboratory-reared males of *Amarinus lacustris* and *A. paralacustris* up to three instars before their pubertal moult successfully impregnated females (Lucas, 1968). Copulating pairs of *A. laevis* collected in the field included large prepubertal males (Lucas and Hodgkin, 1970a). Richer de Forges (1977) observed copulation by prepubertal males of *Halicarcinus planatus*. Successful copulation by late prepubertal males is possible because their intromittent organs, the 1st and 2nd pleopods, are in an essentially mature condition.

After its onset, several instars before the pubertal moult, spermatogenesis may continue for long periods. Individual males of *Amarinus lacustris* and *A. paralacustris* were used for a number of successful impregnations over periods of months (Lucas, 1968). One male of the latter species was used for twelve impregnations over a period of 16 months. Broekhuysen (1955) found apparent seasonallity in testis size in a *Hymenosoma orbiculare* population, but this may be related to the annual cycle of recruitment in the Sand Vlei estuary, South Africa.

Copulation in Brachyura always involves a hard-shelled male and Hartnoll (1969) distinguished two patterns of copulation according to shell condition of the female. In one pattern the female is soft-shelled and copulation is usually preceded by lengthy premoult courtship; in the other pattern the female is hard-shelled and there is relatively brief courtship. Both patterns have been reported for hymenosomatids (Table 3) and they may both occur in one species, e.g. *Halicarcinus ovatus*. The requirement for females to be soft-shelled for copulation severely limits the period available for copulation. This is not so critical for *Hymenosoma orbiculare*, females of which continue to moult after their

TABLE 3. Shell condition of female in copulation. F — observed in field. L — observed in laboratory.

| | Female | | |
|---|---|---|---|
| **Species** | **Soft-shelled** | **Hard-shelled** | **Source** |
| *Amarinus lacustris* | L | L* | Lucas (1968) |
| *A. paralacustris* | L | L* | Lucas (1968) |
| *A. laevis* | F | | Lucas and Hodgkin (1970a) |
| *Halicarcinus ovatus* | L | L | Lucas (1968) |
| *H. rostratus* | L | | Lucas (1968) |
| *H. cookii* | | L | Melrose (1975) |
| *H. planatus* | | L | Richer de Forges (1977) |
| *Hymenosoma orbiculare* | L | | Broekhuysen (1955) |

* This only was observed at times when a male was introduced into a small container with a solitary female; the females were apparently not successfully impregnated since they produced inviable egg masses.

pubertal moult giving opportunities for impregnation or re-impregnation. However, in species of *Amarinus* and *Halicarcinus,* which have a pubertal/terminal moult and which may only copulate while the female is soft-shelled, the period immediately following the pubertal moult is critical as the last opportunity for impregnation.

Hymenosomatid females may extrude eggs within a day or two after their pubertal moult and after release of larvae from the previous egg mass. As a result of this pattern of egg masses in close succession, females may be ovigerous for most of their reproductive life and high proportions of mature females in hymenosomatid populations may be ovigerous. In the Material Examined for *Halicarcinus ovatus,* representing a number of collections from different Australian localities, there are 52 ovigerous females of a total of 64 mature females. All 33 mature females of *H. bedfordi* examined during this study were ovigerous. Where Melrose (1975) examined a large number of specimens of a *Halicarcinus* or *Elamena* species from New Zealand, these included a high proportion of ovigerous females among mature females. Almost all mature females of *Halicarcinus planatus* were ovigerous throughout the autumn to spring breeding season at Kerguelen Island (Richer de Forges, 1977). More than 70% of females, mature or immature, of *Hymenosoma orbiculare* were ovigerous from July to October in the Sand Vlei estuary, South Africa (Broekhuysen, 1955). Most mature females of *Amarinus laevis* are ovigerous during the summer breeding season in the Swan estuary, Western Australia (Lucas and Hodgkin, 1970a), but, if females reach maturity before summer, they delay extrusion of eggs for several months.

*Amarinus paralacustris* females reared in the laboratory first extruded eggs within 36 hours of their pubertal moult, whether copulation occurred or not (Lucas, 1968). They then extruded successive egg masses within 24 hours of release of larvae from the previous egg mass until the female died or her ovarian cycle ceased. In seven females the number of successive egg masses produced was four to 14, with a mean of eight (Lucas, 1968). There was no seasonal suppression of the ovarian cycle in these laboratory animals. Ovulation appeared to be total, with the ovaries (visible through the translucent carapace in laboratory animals) being very small after ovulation and egg extrusion. The ovaries increased in size progressively during the period of embryonic development of the concurrent egg mass in the abdominosternal cavity. They reached maximum size shortly before larval release. Since ovulation and extrusion of eggs occur so soon after larval release, the stimulus for ovulation and extrusion of eggs must be related to the events of larval release to achieve this synchronisation.

*Amarinus lacustris* females reared in the laboratory also extruded eggs soon after their pubertal moult (Lucas, 1968). Thereafter ovulations and extrusions of eggs generally followed release of juveniles from the previous egg mass. The ovarian cycle is similar to *A. paralacustris* except the period of embryonic development is much longer in *A. lacustris* and the ovarian cycle is correspondingly longer. The number of successive egg masses produced per female ranged from one to four with a mean of 2.6 for 10 females. In three females the ovarian cycle lapsed and recommenced, resulting in periods of more than 100 days between successive ovulations.

Because of the pattern of successive egg masses during the mature life of females, there is usually a prolonged breeding season in hymenosomatid populations. Ovigerous females have been collected throughout the year from *Halicarcinus ovatus* populations near Perth, Western Australia (Lucas, 1968), and in the following New Zealand species which are well represented in collections: *Halicarcinus cookii, H. varius, H. whitei, H. planatus* (subantarctic), *Neohymenicus pubescens* and *Elamena producta* (Melrose, 1975). Although these species do not have discrete breeding seasons, reproductive effort may be more intense in one part of the year. The abundance of *H. ovatus* larvae in the plankton of Cockburn Sound, Western Australia, was greatest in summer (Lucas, 1975). The proportions of ovigerous females in populations of *H. cookii* at Leigh and Coromandel, New Zealand, were highest in summer, January-February (Melrose, 1975). The proportion of mature females which were ovigerous was highest in winter, April-August, in *H. planatus* populations at Kerguelen Island (Richer de Forges, 1977). Even in the estuarine species, *Hymenosoma orbiculare* and *Amarinus laevis,* ovigerous females occur through most of the year, despite marked seasonal variation in salinity (Broekhuysen, 1955; Lucas and Hodgkin, 1970a). In populations of a freshwater species, *Amarinus lacustris,* at Skeleton Creek, Victoria, there were ovigerous females from July to February (Walker, 1969).

Broekhuysen (1955:324) and Lucas (1968: Table 5.4) described the embryonic development of *Hymenosoma orbiculare* and *A. laevis,* respectively, which follows the pattern of other brachyuran embryos, e.g. Hiatt (1948). Mean periods of embryonic development at 20 ± 1°C are 29, 29, 25.5 and 54.5 days for *Halicarcinus ovatus, Amarinus laevis, A. paralacustris* and *A. lacustris,* respectively (Lucas, 1968). The much longer period of embryonic development in *A. lacustris* results from suppression of free larval stages. Embryonic development of *Hymenosoma orbiculare* takes approximately 43 days at 13°C (Broekhuysen, 1955).

The morphology of the female reproductive system of *Elamenopsis* species is unique (see Remarks on this genus) and they are excluded from the following paragraph discussing ventilation of egg masses. The mechanisms of ovulation, egg ventilation and larval release need to be elucidated in the *Elamenopsis* species.

Ovigerous hymenosomatid females carry their eggs on the endopodites of their four pairs of pleopods. The egg mass in usually competely enclosed between the abdomen and thoracic sternites (some very small *Halicarcinus* and *Elamena* species are exceptional). The female may bend her abdomen away from the sternum to expose the egg mass for inspection and larval release, but most of the time the egg mass is totally enclosed within the abdominosternal (brood) cavity. Branchiosternal canals connect the brood cavity to the branchial chambers in these females. A branchiosternal canal leads from each of two sternal apertures at the junction of the last thoracic sternite and first abdominal sternite. Pericardial sacs extend along the canals and water currents flowing through the canals were demonstrated using dye in mature females of three *Amarinus* species and *Halicarcinus ovatus* (Lucas, 1968). The current flows from the brood cavity to the branchial chambers and its function must be to irrigate the egg mass (Lucas, 1968). Branchiosternal canals are present in females of other brachyuran families (Lucas, unpubl. data), but they appear to have been described in only one other family, the Leucosiidae (Drach, 1955). Drach found a water current flowing through the canals from the branchial chambers to the brood cavity in leucosiid females, due to piston-like pumping of the elongate pericardial sacs. The direction of flow in leucosiids is opposite to that in hymenosomatids, but Drach (1955) also proposed that it ventilates the egg mass in ovigerous females. It is necessary in leucosiids, as in hymenosomatids, because the abdomen is held against the sternum, restricting water change between the environment and the egg mass.

Spermatozoa storage has been conclusively shown in some hymenosomatids. Females of *Amarinus lacustris, A. paralacustris* and hybrids from them produced series of fertile egg masses without further impregnation after one post-puberty impregnation (Lucas, 1968). One hybrid female produced fifteen viable egg masses in succession after one impregnation. Among these females there was a trend of declining numbers of larvae from successive egg masses, apparently due to decreasing proportions of fertilized eggs, until the female began rejecting all eggs from each ovulation. *A. laevis* and *Halicarcinus* *ovatus* also produced viable egg masses in the laboratory without re-impregnation. Broekhuysen (1955) showed spermatozoa storage, including trans-moult retention of spermatozoa, in *Hymenosoma orbiculare* in the laboratory. As in other female Brachyura, spermatozoa are stored in the spermatheca which is an enlarged region of the genital duct between the vagina and the oviduct (Hartnoll, 1968). The spermatozoa are densely scattered in a noncellular matrix that fills the lumen of the spermatheca in *Amarinus lacustris* and *A. laevis* (Lucas, 1968). The spermatozoa of these species are spherical to ovoid, 2.2-3.3 μm in size; they are densely basophilic and have little cytoplasm. Eggs are fertilized between ovulation and extrusion in the lumen of the ovary or in the oviduct (Cheung, 1966b). Hartnoll (1966) briefly considers the female genital ducts of *Halicarcinus planatus* in relation to general patterns in Brachyura with sternal apertures.

## REPRODUCTIVE STRATEGIES

The family Hymenosomatidae includes some of the smallest, if not the smallest, species of Brachuyra. There has obviously been selection pressure for smallness; but, whatever the advantages of small size in this family, there is one potential disadvantage. Small size means small amounts of energy and material available for reproduction. Also, in these crabs fecundity is futher limited by the necessity to produce relatively large eggs, which support extensive embryonic development, and by the necessity to retain extruded eggs until they hatch. Brachyuran eggs give rise to large advanced larvae or juvenile crabs; the eggs require ventilation and maternal care to survive the long period of embryonic development and thus they are attached to the body of the female. It would be a very radical change for hymenosomatids to deviate from this pattern to increase fecundity, e.g. to revert to nauplius larvae hatching from small planktonic eggs, as in penaeid decapods. The hymenosomatids do not show radical modifications of the brachyuran pattern of reproduction and development, but they show several reproductive strategies to increase fecundity and to promote survival of their early developmental stages.

Adaptions of hymenosomatids to increase fecundity are:—

(i) **Reduced egg size:** Reducing egg size results in more eggs per unit expenditure of energy and material. However, there is a lower limit to the size of an egg which gives rise to a functional zoea larva. Many hymenosomatids may be close to the limit: their eggs and their larvae are among the smallest in the Brachyura. The *Elamenopsis* species and smaller *Halicarcinus* and *Elamena* species have eggs less than 0.3 mm diameter; the smallest egg reported is 0.23 mm for *Halicarcinus hondai.*

(ii) **Increased volume of the brood cavity:** This allows more eggs to be carried and, as a corequisite, the female must be able to increase the volume of eggs produced per ovulation.

In most female hymenosomatids the edge of the abdomen fits closely to the thoracic sternum to make an enclosed brood cavity. However, in the very small species, *Halicarcinus hondai, H. keijibabai, Elamena gordonae* and *E. umerata,* the abdomen is wider than the cephalothorax and/or the pleopods project laterally beyond the abdomen, giving a greater volume for egg bearing. The condition of the abdomen is similar to that in symbiotic pinnotherid females. (It would be interesting to know more of the habitats and habits of these hymenosomatid species, because their very large abdomens must restrict locomotion.) In *H. hondai,* at least, the ovaries appear to extend into the abdomen to increase the volume of eggs produced per ovulation.

In two *Hymenosoma* species the female abdomen projects posteriorly, increasing the volume of the brood cavity without interfering with the walking legs. In *Elamenopsis* species a brood cavity extending from within the abdomen to within the cephalothorax completely replaces the abdominosternal cavity, apparently to increase the volume for bearing eggs (Fig. 8H).

(iii) **Many egg masses:** A characteristic of hymenosomatid populations, discussed in the Reproduction section, is the high proportion of mature females which are ovigerous through much of the year. This results from successive extrusions of egg masses, often within a day or two of liberation of larvae from the previous egg mass. Thus females may be ovigerous for most of their mature lives. The common pubertal/terminal moult in at least *Amarinus* and *Halicarcinus* species is an advantage for egg mass production because the ovarian cycle can continue without interruption by moulting cycles, see Cheung (1966a).

Although hymenosomatids show adaptions to increase fecundity, this is within the constraints of their small size. Data on numbers of eggs carried per egg mass by females are presented in Table 4. The range for hymenosomatid species with larval development is from less than 100 eggs per egg mass to unit thousands per egg mass. By comparison, a moderate sized grapsid, *Pachygrapsus crassipes,* 36.5 mm carapace width, carries 48,600 eggs (Hiatt, 1948) and a large portunid, *Scylla serrata,* 131 mm carapace width, carries 2,012,000 eggs per egg mass (Arriola, 1949). Even allowing that hymenosomatids may produce more egg masses per female, or per unit time, than most Brachyura their total fecundity must be in the lower range for the Brachyura. In fact their fecundity is at the lower extreme of the range of average numbers of eggs spawned by benthic marine invertebrates with planktotrophic larvae. Thorson (1950) gave values of $1.1 \times 10^3$ to $5 \times 10^8$ eggs per female for this range, but the smaller hymenosomatids fall below $1.1 \times 10^3$ eggs. Thus hymenosomatids must achieve much higher rates of larval survival and higher rates of recruitment from pelagic to benthic populations than most benthic marine invertebrates with planktotrophic larvae.

TABLE 4. Approximate numbers of eggs per egg mass in ovigerous hymenosomatid females from marine and brackish environments.

| **Species** | **Carapace width (mm)** | **Number of eggs** | **Source** |
|---|---|---|---|
| *Amarinus laevis* | 16.0 | 3,200 | Lucas (1968) |
| *Halicarcinus planatus* | 13.7 | 1,400 | Richer de Forges (1977) |
| *Halicarcinus ovatus* | 6.5 | 850 | Lucas (1975) |
| *Amarinus paralacustris* | 6.0 | 400 | Lucas (1970) |
| *Halicarcinus rostratus* | 4.0 | 250 | Lucas (1975) |
| *Elamenopsis lineata* | 3.7 | 130 | Lucas (unpubl.) |
| *Elamenopsis aspinifera* | 3.0 | 77 | Lucas (unpubl.) |
| *Elamenopsis bovis* | 5.5 | 30* | Barnard (1950) |
| *Halicarcinus afecundus* | 5.4 | 24** | this study |

* direct development
** direct development suspected

Adaptations by hymenosomatids to promote survival of their larvae are:—

(i) **Abbreviated larval development:** Reducing the period of planktonic larval development reduces mortality from plankton predators, unfavourable dispersal and other sources of larval mortality (reviewed by Thorson, 1950). Conversely, the advantages of planktotrophic development, dispersal and exploitation of an alternative food source, are reduced.

The larval development of hymenosomatids is abbreviated compared to other Brachyura and most other decapod Crustacea, consisting of only three zoeal stages and no megalopa stage. Duration of larval development has only been studied in a few species and it is relatively brief, with the exception of the subantarctic *Halicarcinus planatus* (Lucas, 1972; Richer de Forges, 1977).

The extreme case of abbreviated larval development is direct development, i.e. retention of all larval stages within the egg or within the brood cavity of the female. Direct development or near direct development occurs only rarely in marine Brachyura. It has been recorded only from Australian and New Zealand Brachyura in some species of Dromiidae, Majidae and Xanthidae (Wear, 1967). Direct development offers the advantage of omitting the high mortality of planktonic life; although it is at the price of reduced fecundity, because larger yolkier eggs must be produced, and at the price of reduced dispersal. In the balance of advantages and disadvantages of direct development, it would be surprising to find that no hymenosomatids have adapted direct development, since they must achieve particularly high rates of survival through early development. Yet among marine and brackish water hymenosomatids, only one species is known to have direct development: a female of *Elamenopsis bovis* had juveniles in its brood cavity (Barnard, 1950). Another species, *Halicarcinus afecundus* is suspected of direct development from the number and size of eggs on the female holotype (see Remarks on this species and Table 4).

(ii) **Restricted dispersal:** Wide dispersal of planktonic larvae is advantageous for finding new habitats and exploiting all suitable habitats in a region. The disadvantage of wide dispersal is large wastage of larvae through dispersal to unfavourable regions (Thorson, 1950). Species with low fecundity may not be able to afford wide dispersal of their larvae and it would be advantageous if most larvae remain in, or return to, the vicinity of the adult populations from where they were released. Efford (1970) suggested four types of field situation where this would occur.

Most hymenosomatids occur in shallow coastal waters. Although they may occur on exposed coasts, they tend to be most abundant in sheltered coastal localities, in bays, inlets, sounds and estuaries. These semi-enclosed water masses provide protected habitats for the crab populations. But another feature of these localities is that water exchange with the adjacent ocean may be limited by the geomorphology, and dispersal of larvae reduced.

Lucas (1975) investigated the dispersal of larvae of *Halicarcinus ovatus* and *H. rostratus* in Cockburn Sound, Western Australia, which is typical of the type of semi-enclosed locality where these species are most abundant. There were very high rates of retention of larvae within the Sound: overall ratios of numbers of third stage zoeae to first stage zoeae were 0.4:1 and 0.59:1 in plankton samples throughout a year. All three zoeal stages were obtained in the vicinity of crab populations at several other localities where these species are abundant. Lucas (1975) concluded that a major factor in the abundance of *H. ovatus* and *H. rostratus* in semi-enclosed localities is that these localities restrict dispersal of larvae away from the adult habitat. At these localities the small crabs can compensate for their low fecundity with relatively high rates of recruitment. These localities act as "nursery areas", one of the suggested field situations of Efford (1970).

The conclusions for *Halicarcinus ovatus* and *H. rostratus* may be relevant to many other hymenosomatids which are most abundant in protected coastal localities and estuaries. In fact, the absence of a megalopa stage in the development of hymenosomatids may reflect a general strategy of retaining larvae in the vicinity of crab populations. Where the phase of planktonic development is completed in the vicinity of the benthic crab populations the transition from plankton to benthos is rapid. There is no need for a transitionary larval stage, the megalopa, to locate the adult habitat.

## BEHAVIOUR

The major source of data on the behaviour of hymenosomatids is Melrose (1975). Melrose gave detailed observations on various aspects of the behaviour of some New Zealand species, *Halicarcinus innominatus, H. cookii, H. whitei, H. varius, Neohymenicus pubescens* and *Elamena producta*. Lucas (1968) included some data on the behaviour of *Amarinus* species and there are several other brief descriptions of hymenosomatid behaviour. There are, unfortunately, no observations on the behaviour of any species of the largest genus, *Elamenopsis*.

**Locomotion:** Hymenosomatids tend to walk forward, but they are not restricted to this direction. Some species, such as *Halicarcinus cookii,* walk rapidly for short periods; others, such as *Neohymenicus pubescens,* walk slowly and this is more typical of hymenosomatid species. Where males have very large chelipeds these may regularly contact the ground and be used in walking. Melrose (1975) studied the sequence of leg movements during forward walking in the slow-moving *Neohymenicus pubescens*. There was a general pattern of walking leg movements R1, L1, R3 and L3 alternating with R2, L2, R4, L4. Each pair of legs was almost in phase on both sides of the body, both being propulsive together, but no two legs appeared to be exactly in phase. Also, the pattern would alter at random.

Hymenosomatids may also swim, an activity involving much more rapid movements than walking. In swimming the chelipeds are held forward and bent; the walking legs are held laterally and they beat vigorously out of phase in a vertical or slightly backward plane. There are rows of ventrolateral setae on the walking legs and these fold together on the upward recovery stroke and spread on the downward power stroke (Hartnoll, 1971). The crab moves upward or upward and forward, usually with the body in a normal horizontal plane, but sometimes tumbling "head-over-tail" in small crabs. Swimming is most prevalent in early crab instars, especially the first crab instar where it may assist in substrate selection (Lucas, 1968). Some adult hymenosomatids with long setae on their walking legs are well adapted for swimming and often swim for locomotion. These are *Hymenosoma depressum, H. orbiculare* and *Halicarcinus whitei* (Graham, 1938; Barnard, 1950; Melrose, 1975). Other adult hymenosomatids, *Amarinus laevis, A. lacustris, Halicarcinus ovatus, H. varius, H. cookii* and *Neohymenicus pubescens,* swim only as an escape reaction when disturbed or when in unfavourable conditions such as near-lethal water temperature or deoxygenated water (Hartnoll, 1971). Others, *Halicarcinus innominatus* and *Elamena producta,* have not been seen swimming (Melrose, 1975).

**Thigmotaxis:** Hymenosomatids are strongly thigmotactic beginning at the first crab instar. If a group of first instar crabs is kept in a glass vessel without any object for attachment they form a tight bundle of bodies as they cling to each other (Lucas, 1968). Adult crabs will similarly cling to each other if there is no substrate to hold with their walking legs or to burrow into (Melrose, 1975). They may show selection for the type of substrate which they hold: *Halicarcinus cookii* is highly selective for finely divided algae when given a choice of substrates (Melrose, 1975).

**Burrowing:** *Hymenosoma orbiculare, Halicarcinus varius, H. whitei* and *Elamena producta* are known to burrow in sandy to muddy substrates (Barnard, 1950; Melrose, 1975). No permanent burrows are constructed. The crab burrows by digging the posterior of the cephalothorax into the substrate with thrusting movements of the walking legs. It is a gradual process and not a flurry of digging (Melrose, 1975).

**Alarm:** If repeatedly prodded or lifted from the substrate, hymenosomatids become immobile. *Halicarcinus whitei* "freezes" in a normal posture; *H. innominatus, H. cookii, Neohymenicus pubescens* and *Amarinus laevis* "freeze" with their walking legs tightly folded under their cephalothorax; and *Elamena producta* and *E. abrolhensis* "freeze" with their chelipeds and walking legs projecting out laterally (Melrose, 1975; Lucas, unpubl. data).

**Display:** Large males of some hymenosomatid species are more conspicuously patterned than females, suggesting visual display. Large males of most species have relatively large chelipeds and in some species the males have been observed using their chelipeds in threatening displays. The male usually postures with the anterior of the body raised and with its chelipeds held high and wavering or with its chelipeds spread laterally and fingers gaping (Melrose, 1975). Males of two species which use the spread chelipeds display, *Halicarcinus varius* and *H. whitei*, engage in intraspecific agonistic display, facing each other with chelipeds spread and with the anterior surfaces of the palms touching those of the other male (Melrose, 1975). Males of *H. innominatus*, which use the waving cheliped threat display, grip each other's chelae in some agonistic displays. *Neohymenicus pubescens* and *Elamena producta* show no reaction to other males (Melrose, 1975).

In these limited data on display there is considerable variation among related species.

**Courtship:** In hymenosomatids, copulations may involve hard-shell or soft-shell females (Table 3) and several patterns of courtship and post-copulatory behaviour have been reported. As in other Brachyura, only hard-shell males are involved in mating behaviour.

In copulation with a hard-shell female of *Halicarcinus cookii* there was no evidence of courtship; the male climbed onto the female, moved beneath her and clasped her above himself (Melrose, 1975). The crabs separated immediately after copulation. In *Hymenosoma orbiculare* only soft-shell females were involved in mating (Broekhuysen, 1955). Copulation was preceded by the male carrying the female beneath him for some time before she moulted. After copulation the male returned to holding the female beneath him for up to a day or longer. These observations accord with the two basic patterns of crab courtship behaviour described by Hartnoll (1969): lengthy pre-moult courtship before mating with soft-shell females and brief courtship before mating with hard-shell females.

No courtship was observed in males of *Amarinus lacustris* and *A. paralacustris* which mated with soft-shell females (Lucas, 1970). However, in most of the observed copulations the male was only given access to the female immediately after her pubertal moult. In this circumstance, the male often gripped the female and manoeuvred her into copulation position at first contact. The copulation position was consistently female-over-male; when on top of their substrate the female gripped it with her walking legs, when on the undersurface of the substrate the male gripped it with several walking legs (Lucas, 1968). The copulation position was held for 10-30 minutes, and then the male manoeuvred the female without releasing her until he was holding her beneath him, both being upright and facing the same direction. This post-copulatory behaviour is the same as in *Hymenosoma orbiculare* and it lasted for several hours to five days in *A. lacustris* and *A. paralacustris*.

Post-copulatory pairing has been reported in some other Brachyura, always in cases of soft-shell female mating (Hartnoll, 1969). Presumably it protects the female (from other males?) until her integument hardens.

**Species recognition:** Lucas (1970) attempted a series of interspecific crosses between *Amarinus lacustris* and *A. paralacustris* using soft-shell females immediately after their pubertal moult. These are very similar species which cannot be distinguished on male morphology. In six out of ten cases where an *A. lacustris* male was introduced to an *A. paralacustris* female or to a hybrid *(A. paralacustris* ♀ x *A. lacustris* ♂*)* female no copulation occurred; the male either ignored the female or mutilated her by tearing off legs after she resisted being manoeuvred. In a cross attempted with a mature soft-shell female of *H. rostratus* and a male of *H. ovatus* no copulation occurred and the male tore legs off the female (Lucas, 1968). Thus there is some species isolation at copulation, either from the male failing to recognise the female as a mating partner or from the female resisting the male. In attempted interspecific crosses where the male mutilated the female, it appeared that initially the male attempted copulation, but the female thwarted him.

Opposed to the data suggesting precise recognition at copulation are various observations of males of *A. lacustris* and *A. paralacustris* which showed no recognition of sex or shell condition. In the laboratory, males attempted copulation and showed post-copulatory pairing with other males, with immature hard-shell females, with exuviae and with ovigerous females (Lucas, 1968). Lack of discrimination was most common in males which had been isolated from females.

## ECOLOGY

Broekhuysen (1955), Lucas and Hodgkin (1970a), Melrose (1975) and Richer de Forges (1977) made population studies of hymenosomatids in marine and estuarine habitats. The most comprehensive of these studies, Lucas and Hodgkin (1970a and b), related the annual cycle of recruitment and growth in *Amarinus laevis* populations in the Swan River estuary to larval survival and seasonal variations in temperature and salinity. Other ecological data on hymenosomatids are scattered through the literature, with Walker (1969), Melrose (1975) and Richer de Forges (1977) being major sources of data on *Amarinus lacustris*, New Zealand hymenosomatids and *Halicarcinus planatus*, respectively. Ecological data for the larval stages of hymenosomatids are contained in Lucas and Hodgkin (1970b) and Lucas (1975).

**Habitats:** The occurrence of hymenosomatid species in freshwater, brackish and marine habitats is summarised in Table 5. As evident from the table, most marine hymenosomatids occur in shallow coastal waters, in the littoral zone or sublittoral to 20m. The deepest record for a hymenosomatid is 494 m for *Halicarcinus tongi* off Mayor Island, New Zealand (see Melrose, 1975:91). *H. tongi* appears to be the only deep water species and the shallowest depth of its collection is 55-73 m. Other hymenosomatids collected from below 100 m depth, *Halicarcinus planatus* (270 m; Garth, 1958), *H. setirostris* (110 m; Takeda 1973), *Elamena longirostris* (90-116 m; Takeda and Miyake, 1969), and *Trigonoplax spathulifera* (128-137 m, this study), also occur in the littoral zone or at less than 30 m depth. Although many hymenosomatid species occur in the littoral zone, none

TABLE 5. Occurrence of hymenosomatid species in freshwater, brackish and marine habitats.

| GENERA | Freshwater | Brackish | Littoral | Marine Sublittoral | | | Total Species |
|---|---|---|---|---|---|---|---|
| | | | | to 20 m | 20-100 m | >100 m | |
| *Trigonoplax* | | | 1 | 3 | 2 | 1 | 3 |
| *Elamena* | | 2 | 6 | 8 | 2 | 1 | 12 + 2* |
| *Halicarcinus* | | 1 | 12 | 8 | 5 | 3 | 15 + 1* |
| *Halimena* | | | 1 | 1 | 1 | | 1 |
| *Halicarcinides* | | | 1 | 1 | | | 1 |
| *Neohymenicus* | | | 1 | 1 | | | 1 |
| *Hymenosoma* | 1 | 1 | 3 | 3 | 1 | | 3 |
| *Elamenopsis* | 3 | 8 | 6 | 1 | 1 | | 16 + 1* |
| *Hymenicoides* | | 1 | | | | | 1 |
| *Amarinus* | 4 | 3 | | | | | 7 |
| TOTAL SPECIES | 8 | 16 | 31 | 26 | 12 | 5 | 64 |

* Insufficient habitat data to include in table

are active out of water. They do not tolerate desiccating conditions for long (Melrose, 1975: Table 3) and they either move out with the tide or conceal themselves in non-desiccating conditions at low tide.

Marine hymenosomatids not only occur most frequently in shallow coastal waters, they tend to be most abundant in protected localities, in bays, sounds and inlets. This is partly because, with the exception of several stout-legged species, e.g. *Halicarcinus planatus* and *H. innominatus,* they avoid conditions of strong wave action. But also it is postulated that these semi-enclosed water masses restrict larval dispersal, permitting high rates of recruitment (see Reproductive strategies section). Because many marine hymenosomatids occur in protected coastal localities they are in the promixity of estuaries and may be exposed to lowered salinity at times of strong freshwater discharge from the land. Thus it is not surprising to find that some hymenosomatids have become brackish water inhabitants (Table 5). The invasion of low salinity environments is considered in the next section.

**Concealment substrates:** A major need of hymenosomatid crabs is an appropriate substrate in which to conceal themselves: they are such small, thin-shelled crabs that they can only avoid large predators by being inconspicuous and inaccessible. Hymenosomatids hide in a great range of aquatic substrates: in filamentous and coralline algae, among algal holdfasts, in mussel beds between empty valves or among byssal threads, among ascidians, sponges and bryozoans, among marine angiosperm roots and branches, under rocks, in coral rubble, in plant debris and buried in mud, silt and fine sand. Each species occurs on particular substrates and certain morphological features can be related to the type of substrate inhabited by the crab. Species occurring on soft substrates tend to have slender legs, while those occurring on hard substrates, and in turbulent conditions, tend to have stouter legs. Species occurring on filamentous algae tend to have well developed spines on the body and well developed teeth on the dactyli of their walking legs. Species occurring on silty and muddy substrates tend to have a shield-like rostrum, they tend to be hairy and they have few teeth on the dactyli of their walking legs. Species which inhabit algae and brightly coloured substrates tend to have brighter and more varied pigmentation than species in silty and muddy habitats. The latter species tend to be uniformly brown.

Hairiness of the body surface leads to accumulation of fine particles which helps to camouflage the crab in muddy and silty habitats. Patterns of chromatophores on the body surface assist in camouflage and light/dark adaptation of chromatophores has been shown in *Halicarcinus cookii* (Melrose, 1975).

**Density:** Although the hymenosomatid crabs are never conspicuous members of benthic communities, careful collecting may reveal that they are quite abundant. Density data on hymenosomatid crabs in various habitats are presented in Table 6. Cassie and Michael (1968) found a community on an intertidal mud flat which was characterised by *Halicarcinus cookii* and a tubiculous polychaete. Obviously *H. cookii* was abundant, but Cassie and Michael do not give density data.

The abundance of hymenosomatid larvae in Cockburn Sound, Western Australia, is a further example of their density at favourable localities. In plankton samples over a year at two inshore stations there were as many hymenosomatid larvae as all other brachyuran larvae combined (Lucas, 1975).

**Food:** Analyses of the gut contents of some hymenosomatid crabs show that they are omnivores. A major component of their gut contents is debris, mainly plant material, which has been masticated by the mouthparts and gastric mill. In addition to debris,

TABLE 6. Densities of hymenosomatid species in various habitats.

| **Species** | **No./0.1m$^2$** | **Substrate** | **Source** |
|---|---|---|---|
| *Halicarcinus cookii* | 2-4 | *Corallina* turf | Melrose (1975) |
| *H. innominatus* | 10-15 | mussel beds | Melrose (1975) |
| *H. innominatus* | 3-4 | littoral pools | Melrose (1975) |
| *H. whitei* | 0.8 | sand | Melrose (1975) |
| *H. varius* | 4-6 | *Sargassum* | Melrose (1975) |
| *H. varius* | 4 | sheltered beach | Wood (1968) |
| *H. varius* | 12 | *Zostera* flat | Wood (1968) |
| *H. planatus* | 2.3-13.5 | mussel beds | Richer de Forges (1977) |
| *H. rostratus* | 1-16 | *Heterozostera* | Littlejohn (unpubl.) |
| *H. ovatus* | 1-11 | *Heterozostera* | Littlejohn (unpubl.) |
| *Hymenosoma orbiculare* | 0.2 | lake bottom | Boltt (1969) |
| *Neohymenicus pubescens* | 2-6 | reef platform | Melrose (1975) |

Lucas (1968) found crustacean remains, including amphipods, in *Amarinus laevis, A. lacustris* and *Halicarcinus ovatus*; Walker (1969) found amphipod remains, algal strands and root fibres in *Amarinus lacustris;* and Richer de Forges (1977) found sand particles, shell fragments, remnants of algae, diatoms, polychaete setae, and fragments of copepods and isopods in gut contents of *Halicarcinus planatus*. The animal remains may result from capture of live prey. *Amarinus lacustris, A. paralacustris,* small *A. laevis* and *Halicarcinus* ovatus captured live *Artemia salina* nauplii in the laboratory and the first two species and hybrids were reared through successive generations with *Artemia* nauplii as sole food source (Lucas, 1968). Melrose (1975) found that *Halicarcinus cookii, H. varius, H. whitei* and *E. producta* captured live amphipods and polychaetes in aquaria. Some *H. cookii* and *E. producta* required moving prey to initiate their capture behaviour. Prey were captured as the crab waited in an alert posture and then seized the prey in its chelae as the prey passed in front of the crab (Melrose, 1975); or, for feeding on *Artemia* nauplii, as the prey swam into contract with the inner surfaces of the walking legs (Lucas, unpubl. data). In the former case the crabs responded to visual perception, in the latter to tactile perception.

*Halicarcinus cookii, H. varius* and *H. whitei* ate algae or *Zostera* when deprived of prey (Melrose, 1975) and several other food sources and modes of feeding have been described for hymenosomatids. *H. whitei* scooped sand into its mouthparts, apparently extracting organic material, as well as being predatory and eating macroscopic plant material; *H. innominatus* preferred dead animal flesh and entered the valves of decaying mussels; *Neohymenicus pubescens* ate sponge and appeared to filter feed with its hairy mouthparts (Melrose, 1975). *Hymenosoma orbiculare* was observed feeding by probing sandy substrates with its chelipeds and it was presumed to feed on interstitial crustaceans (Boltt, 1969).

**Symbioses:** No hymenosomatids are known to deliberately mask their bodies with biological material, but their cuticles tend to collect epizooites. These are most common in mature crabs after their terminal moult because of the long period without moulting. Epizooites reported from hymenosomatids are sessile Protozoa, sponges, small anemones, nematodes, serpulids, cirripeds and Bryozoa (Lucas, 1968; Melrose, 1975; Richer de Forges, 1977). Garth et al. (1967) and Richer de Forges (1977) report specimens of *Halicarcinus planatus* with rhizocephalan parasites. Lucas (1968) found bivalved organisms in the abdominosternal region and penetrating the body cavity of *Amarinus lacustris* males.

As well as the above cases of symbioses where the crabs act as hosts, three hymenosomatid species possibly use larger invertebrates as hosts in symbiotic relationships. The hosts in each case are echinoderms. *Elamenopsis ariakensis* is commensal with the holothurian, *Protankyra bidentata* (Woodward and Barrett) on mud flats at Shimabara, Nagasaki Prefecture, Japan (Sakai, 1969). Unfortunately, Sakai does not explain the nature of the commensalism and, as only a few specimens have been reported, it is not clear that the crab is invariably associated with the holothurian. Shen (1932) notes that *Elamenopsis sinensis* is found under stones and "sometimes attached on sea urchins". This may be a casual relationship with the crab using the echinoid as nothing more than one of its concealment substrates, just as other hymenosomatids conceal themselves among sessile invertebrates. Takeda et al. (1976) found *Halicarcinus orientalis* associated with an ophiuroid, *Ophiocoma brevipes* Peters at Hachijs Island, southern Japan. The crabs clung to the oral surface of the ophiuroid in the vicinity of the disc. Usually one, but sometimes two, crabs occurred on one ophiuroid; and, at two shallow localities, one in three and one in ten ophiuroids had crabs on them. The crabs remained in place as the ophiuroid moved. Considering their position, it is possible that the crabs obtained food from their host through its feeding or defaecation. *H. orientalis* is known from other localities as a free-living species occurring under rocks and among algae in the littoral and shallow sublittoral zones (Sakai, 1938, 1965).

**Predators:** Analyses of gut content of New Zealand fish show that many fish prey on hymenosomatid crabs and that hymenosomatids are an important component of the diets of fish feeding on the benthos. Of 52 species of elasmobranch and teleost fish which fed on crabs, 26 species contained hymenosomatids in their gut contents (Graham, 1938; Godfriaux, 1969). One hymenosomatid species, *Hymenosoma depressum,* occurred in gut contents of 23 fish species. In terms of number of fish species for which it served as food, *H. depressum* was the second most important species of Brachyura in New Zealand (Graham, 1938). (The abundance of *H. depressum* in fish gut contents is in contrast to the low numbers in Museum collections, see Melrose (1975).) In snapper, *Chrysophrys auratus* (Block and Schneider), specimens of *H. depressum* were most common in fish from shallow muddy habitats near estuaries and more abundant in gut contents of female fish than in male fish (Godfriaux, 1969).

*Hymenosoma orbiculare* is heavily preyed on by fish, in particular *Clarias gariepennis,* in Lake Sibayi, South Africa (Boltt, 1969). All teleost fish feeding on the benthos at Kerguelen Island prey on *Halicarcinus planatus* at least occasionally and some fish have *H. planatus* as a major component of their diet (Richer de Forges, 1977). Rays, *Raja* spp., also prey on *H. planatus.* Probably the largest number of hymenosomatids recorded from a fish's gut contents is 54 specimens of *Amarinus laevis* recorded from a brown trout, *Salmo trutta,* in the Derwent River, Tasmania (see Material Examined for *A. laevis*).

Sea birds which feed in the littoral zone may also prey on hymenosomatids (Richer de Forges, 1977).

Richer de Forges (1977) concluded from his study at Kerguelen Island that *Halicarcinus planatus* plays a fairly important role in food webs. Considering the reported densities of hymenosomatid crabs in some habitats and their frequent occurrence in fish gut contents from some localities, it is probable that hymenosomatids play a significant role in food webs in marine, brackish and freshwater habitats at other localities, at least in New Zealand, southern Australia and southern Africa.

## INVASION OF LOW SALINITY HABITATS

Previous authors have remarked on the occurrence of hymenosomatids in low salinity habitats, e.g. Kemp (1917), Chopra and Das (1930), Balss (1934) and Holthuis (1968). But only after tabulation of the distribution of hymenosomatid species in various habitats (Table 5) has the high proportion of species in low salinity habitats become evident. Eight species occur in permanent fresh water: *Hymenosoma orbiculare* (Lake Sibayi population), *Elamenopsis introversus, E. kempi, E. inermis, Amarinus lacustris, A. woltereck*i, *A. pilosus* and *A. angelicus.* Twenty three of the 64 hymenosomatid species, i.e. 36% of the species, inhabit low salinity waters, either fresh water or brackish water that may vary between fresh and marine salinity. Six genera, including all the multispecific genera except *Trigonoplax,* contain species inhabiting low salinity waters, suggesting that there has been a number of independent invasions of non-marine habitats. This assumes that the hymenosomatids are primarily marine, which is a very reasonable assumption considering the habitats of related Brachyura, i.e. other Oxyrhyncha or the Pinnotheridae and Leucosiidae, which have also been suggested as relatives of the hymenosomatids. There is no fossil record of the Hymenosomatidae (Glaessner, pers. comm.) to illuminate their ancestry. The family apparently originated in Tertiary-Recent times and the process of evolution into low salinity habitats may still be proceeding. Two species, *Amarinus lacustris* and *Hymenosoma orbiculare,* have recently invaded freshwater habitats (Allanson, et al., 1966; Lucas, 1970). Five or six hymenosomatid species have populations occurring permanently in brackish water, while other populations occur in essentially marine conditions; the different populations may be physiological races (cf. Dorgelo, 1976).

As described in the previous section on Ecology, marine hymenosomatids tend to occur in protected coastal localities where they may experience lowered salinity at times of strong freshwater discharge from the land. Thus, Melrose (1975) recorded habitat salinities down to 30.5, 27.3 and 24°/oo for the marine species *Neohymenicus pubescens, Halicarcinus varius* and *H. innominatus,* respectively. Salinity tolerance experiments provide further evidence of euryhalinity in some marine hymenosomatids. Specimens of *H. cookii* survived indefinitely in 50% seawater; specimens of *H. varius* from two localities survived for mean periods of 6 hours and 6 days in fresh water (the specimens which survived much longer were from a locality where they were normally subject to lowered salinity); specimens of *H. whitei,* which extends into estuaries, survived for a mean period of 10 days in fresh water (Melrose, 1975). Adult crabs of *H. ovatus* survived for more than a week at 27°/oo Sal. without mortality (Lucas, 1968) and first stage zoeae of this species survived for 4-5 days at 21.1°/oo Sal. with little mortality (Lucas, 1972).

In the classification of Crustacea according to their salt tolerance, proposed by Dorgelo (1976), it is likely that the majority of marine hymenosomatids are type II, "more or less euryhaline inhabitants of hyperhaline, marine, intertidal and estuarine environments". The only type I, "polystenohaline, true oceanic", species may be *Halicarcinus tongi* and *Elamena longirostris.* Thus it is not surprising that from this large group of "more or less euryhaline" marine species there has been evolution into habitats of progressively lower and variable salinity.

Osmoregulation has been studied in only one hymenosomatid, *Hymenosoma orbiculare* (Forbes and Hill, 1969). Crabs of this species from an estuarine locality showed the pattern of hyperosmotic regulation in low salinity and hyposmotic regulation in salinities near seawater and more saline, which is typical of euryhaline decapod Crustacea. Lucas (1972) studied physiological adaptations to brackish water in the larval stages of two *Amarinus* species. The periods of larval development of *A. laevis* and *A. paralacustris* were about 9 days shorter than the periods of larval development of two *Halicarcinus* species at the same temperature. This abbreviation of the period of larval development is advantageous in the estuarine habitats of the *Amarinus* species: prolonged larval development is unnecessary for dispersal and it increases the probability of larvae being lost from the estuary or encountering adverse conditions in these characteristically heterogeneous habitats. Further adaptations of *A. laevis* and *A. paralacustris* larvae to brackish conditions are relatively broad salinity and temperature tolerances and tolerance of abrupt salinity changes (Lucas, 1972).

The mode of early development is known for only three of the hymenosomatid species which occur in fresh water. Two of these, *Amarinus lacustris* and *A. angelicus,* have no free larval stages (Lucas, 1971; J. C. Yaldwyn, pers. comm.). Another species, *Elamenopsis kempi,* probably has no free larval stages as it has large eggs, 0.52-0.6 mm diameter (Abele, 1972). This mode of development accords with the trend of suppression of free larval stages among freshwater decapod Crustacea (Gurney, 1942). Lucas (1971, 1972) discusses how suppression of free larval development is related to limited dispersal required in small freshwater habitats, to unsuitability of planktonic stages in running fresh water and to osmoregulatory problems of small larval stages. *Hymenosoma orbiculare,* the other hymenosomatid for which early development is known, has free larval stages in 0.25°/oo Sal. in Lake Sibayi (Allanson et al., 1966; Forbes and Hill, 1969).

TABLE 7. Numbers of species of each hymenosomatid genus in various geographical regions. The numbers in brackets are numbers of species which are endemic to that region; species indicated with an asterisk are probably recent introductions by man. The regions are listed from most northern to southern; they are explained further in the text.

| | GENERA | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Region › | *Hymenosoma* | *Elamena* | *Halicarcinus* | *Trigonoplax* | *Elamenopsis* | *Hymenicoides* | *Halimena* | *Amarinus* | *Halicarcinides* | *Neohymenicus* | Total Species |
| Japan | | 1 | 4(2) | 1 | 2(2) | | | | | | 8(4) |
| Red Sea | | 1 | | | 1(1) | | | | | | 2(1) |
| India | | 6(4) | | 1 | 7(6) | 1(1) | | | | | 15(11) |
| Micronesia | | | | | 1(1) | | | | | | 1(1) |
| Indo-Malaya | | 1 | 3 | 1 | 4(2) | | | 1(1) | | | 10(3) |
| Cen. America | | | | | 1* | | | | | | 1* |
| W. Africa | | 1 | | | | | | | | | 1 |
| S.E. Africa | 1 | 2 | | | | | | | | | 3 |
| N. Australia | | 3(1) | 5(3) | 1(1) | 4(2) | | | 4(3) | | | 17(10) |
| S. Australia | 1(1) | 1(1) | 3+1*(2) | 1(1) | | | | 3(1) | 1(1) | | 10+1*(7) |
| S. Africa | 1 | | | 1 | 1(1) | | | | | | 3(1) |
| New Zealand | 1(1) | 3(3) | 5(5) | | | | 1(1) | 1 | | 1(1) | 12(11) |
| Subantartica | | | 1(1) | | | | | | | | 1(1) |
| TOTAL SPECIES | 3 | 13 | 17 | 3 | 17 | 1 | 1 | 7 | 1 | 1 | 64 |

These larvae warrant further study as there are unusual data relating to them: larvae of *H. orbiculare* from an estuarine locality could not be acclimated to low salinity near that of Lake Sibayi (Forbes and Hill, 1969); *H. orbiculare* larvae in another low salinity lake were collected in grab samples of the benthos at various stations (Boltt, 1975).

## ZOOGEOGRAPHY

Zoogeographical considerations of the family Hymenosomatidae are complicated by the presence of marine, estuarine and freshwater species. Many zoogeographical studies treat marine fauna and fauna of inland waters independently, as different dispersal mechanisms and barriers are involved. However, most of the freshwater hymenosomatid species are closely related to marine species and probably evolved from them quite recently (see previous discussion on invasion of low salinity habitats). For this reason, and for convenience, all species of Hymenosomatidae will be treated together in this brief discussion of their zoogeography.

The distribution of hymenosomatid species is summarised in Table 7. The geographical regions listed in this Table are:
Japan — Japan and northern (temperate) China.
Red Sea — Red Sea and S. W. Asia.
India — India, Pakistan, Bangladesh, Burma and Sri Lanka.
Micronesia.
Indo-Malaya — Indo-Malayan Region defined by Ekman (1967), extending from Ryukyu Islands and southern China through S. E. Asia and the Indo-Malayan archipelago to Kei Islands.
Central America.
Western Africa — tropical coast.
Eastern Africa — tropical coast including Madagascar.
Northern Australia — tropical Australia, Papua-New Guinea and New Caledonia.
Southern Australia — temperate Australia and Lord Howe Island.
Southern Africa — temperate Africa.
New Zealand — New Zealand, adjacent islands and Norfolk Island.
Subantarctica — circum-polar, subantarctic islands and subantarctic region of South America (Magellan Province).

The majority of hymenosomatid species occur in the tropical and sub-tropical shelf waters of the Indo-West Pacific Region and adjacent inland waters. This Region is characterised by a general great diversity of species, even compared to the other shallow-water, tropical Regions of the world, the Eastern Pacific, Western Atlantic and Eastern Atlantic Regions. It is also characterised by a large number of endemic families (Briggs, 1974). The hymenosomatids, although they may well have arisen in the Indo-West Pacific Region, are not endemic to it: a substantial number of species, in eight genera, occur in the temperate and cold-temperate regions to the south.

The hymenosomatids have not dispersed eastward across the Pacific Ocean. In fact, the marine species have not even reached the Central Pacific Islands. This is probably because their brief larval development and low fecundity are unsuited to dispersal over long distances. One exceptional species, *Halicarcinus planatus*, has prolonged larval development because of low environmental temperatures (Boschi et al., 1969; Richer de Forges, 1977) and it has achieved a circum-polar distribution in the Southern and Atlantic Oceans on widely separate land masses. *H. planatus* is one of three hymenosomatid species occurring in the Atlantic Ocean. The other species, *Hymenosoma orbiculare* and *Elamena gordonae*, occur on the west coast of Africa.

Four geographical regions listed in Table 7 have seven or more endemic species. They are India, northern Australia, southern Australia, and New Zealand. The endemic Indian species are mainly species of *Elamena* and *Elamenopsis* in brackish and freshwater habitats, reflecting speciation in non-marine habitats. The hymenosomatid faunas of southern Australia and New Zealand are restricted to one or the other region except for a freshwater species, *Amarinus lacustris,* and a marine species, *Halicarcinus innominatus,* which may have been introduced to Tasmania by man (see Remarks on this species). The Tasman Sea is a very effective isolating mechanism between Australia and New Zealand for the hymenosomatids. There is also an abrupt change in hymenosomatid fauna from southern temperate to northern tropical Australia; only two species, *Amarinus paralacustris* and *Halicarcinus bedfordi,* are common to both regions. Various zoogeographical regions have been proposed for Australia (Ekman, 1967; Briggs, 1974) with a common concept of divisions into northern and southern regions. The poorly-known distributions of marine hymenosomatids in northern Australia correspond approximately to a combination of the Dampierian and Solandarian Regions; the distributions of marine hymenosomatids in southern Australia, which are better known, correspond to a combination of the Peronian and Flindersian Regions.

In contrast to the gererally limited dispersal of marine hymenosomatids across ocean barriers, the freshwater species have been surprisingly successful in crossing these barriers. A freshwater species, *Amarinus lacustris,* occurs in Australia and New Zealand and also on Lord Howe Island and Norfolk Island. It is the only macroscopic, freshwater invertebrate known to occur on all these land masses. Its dispersal to these islands appears to be a recent event since it is genetically compatible with a sibling estuarine species in Australia (see Remarks on *A. lacustris).* Other *Amarinus* species occur in fresh water on isolated land masses: *A. pilosus* in New Caledonia, *A. woltereckí* in Mindanao and *A. angelicus* in the highlands of Papua-New Guinea. A freshwater *Elamenopsis* species, *E. inermis,* is the only hymenosomatid known from Micronesia. None of these freshwater hymenosomatids has related brackish or marine species occurring on the same land mass from which it may have evolved. Their origins and mode of dispersal are problematical considering that they do not have the resistant eggs of some other small freshwater crustaceans (see Remarks on *Amarinus*). There is another extreme case of dispersal of a freshwater hymenosomatid over an ocean barrier: *Elamenopsis kempi* occurs at Basra, Iraq, and in the Panama Canal, Central America, and must have crossed either the Atlantic or the Pacific Ocean. However, its presence in the Panama Canal has been explained as a recent introduction by man (Abele, 1972). *E. kempi* was not collected in the Panama Canal in surveys before 1939. Since then the water plant *Hydrilla* was introduced into the Canal and, as *Hydrilla* occurs in the habitat of *E. kempi* in S.W. Asia, it is possible that they were introduced to the Panama Canal at the same time.

Another unusual distribution of hymenosomatids involves three marine species, each found in northeastern Australia and also at one other locality or region far from Australia. These species are *Elamena gordonae, Halicarcinus hondai* and *Elamenopsis octagonalis,* which are known from western Africa, Ryukyu Island (Japan) and Goa (India), respectively, as well as from northeastern Australia. In each species there are only minor morphological differences between the overseas and Australian specimens and they have not been given subspecific status in view of the small numbers of specimens collected. These may be species which previoulsy had wide geographical distributions, or they may still be widely distributed species for which the two localities or regions of collection are only small parts of their ranges. The three species, like many hymenosomatids, are inconspicuous in size and habit and it is quite probable that they have not yet been collected over most of their geographical ranges.

Almost a quarter of the hymenosomatid species are known only from their type locality; forty per cent of the species are known from three or fewer localities. Of the thirteen geographical regions listed in Table 7, in only three, Japan, southern Australia and New Zealand, have reasonably representative collections been made of the hymenosomatid fauna. In the other regions, with the exception of Central America and Subantarctica, there are likely to be new records and some new species with more adequate collecting. The Indo-Malayan Region, which is central to the geographical distribution of the Hymenosomatidae, is particularly poorly collected.

## ACKNOWLEDGEMENTS

This study was greatly assisted by Mrs M. Melrose's resolution of the taxonomy of New Zealand hymenosomatids and by her lucid drawings of their morphology. I am grateful to Mrs Melrose and to Mr B. Richer de Forges for allowing me access to their unpublished theses. I gratefully thank the following people for making specimens or information available and, in many cases, for generously providing me with facilities at their institutions: Dr D. J. G. Griffin and Dr P. Hutchings (AM), Dr J. S. Garth (AHF), Dr R. W. Ingle (BM), Ms V. A. Wadley (CSIRO), The Commissioner (IFCT), Dr J. Forest (MHN), Mr A. Neboiss (NMV), Mr B. M. Campbell (QM), Dr H. M. Laws (SAM), Mr A. J. Dartnall (TM), Dr R. W. George (WAM), Dr M. Takeda (ZLKU), Dr J. C. Yaldwyn (National Museum of New Zealand), Dr P. Kuenzer (Göttingen Museum), Dr M. Poggesi (Museo Zoologica de "La Specola"), Dr M. J. Littlejohn (University of Melbourne), Mr P. N. Chalmer (University of Western Australia) and Mr W. McCormick (University of New South Wales). I also thank the following people, who assisted in various ways: Mrs M. Chapman, for drawing figures 2-10; Dr J. D. Costlow, Jr., for providing study and typing facilities during my stay at Duke University Marine Laboratory; Dr J. Kohlmeyer, for advice on nomenclature; Mr R. Bodini, Mr R. A. Kenchington, Associate Professor M. Pichon and Dr I. R. Price, for translating papers; Dr R. G. Wear, for allowing me to cite his unpublished work on hymenosomatid larvae and for helpful correspondence.

Financial support for this study was provided by University Research Grants and a Study Leave Grant from James Cook University.

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Manuscript accepted for publication 22 June, 1978.

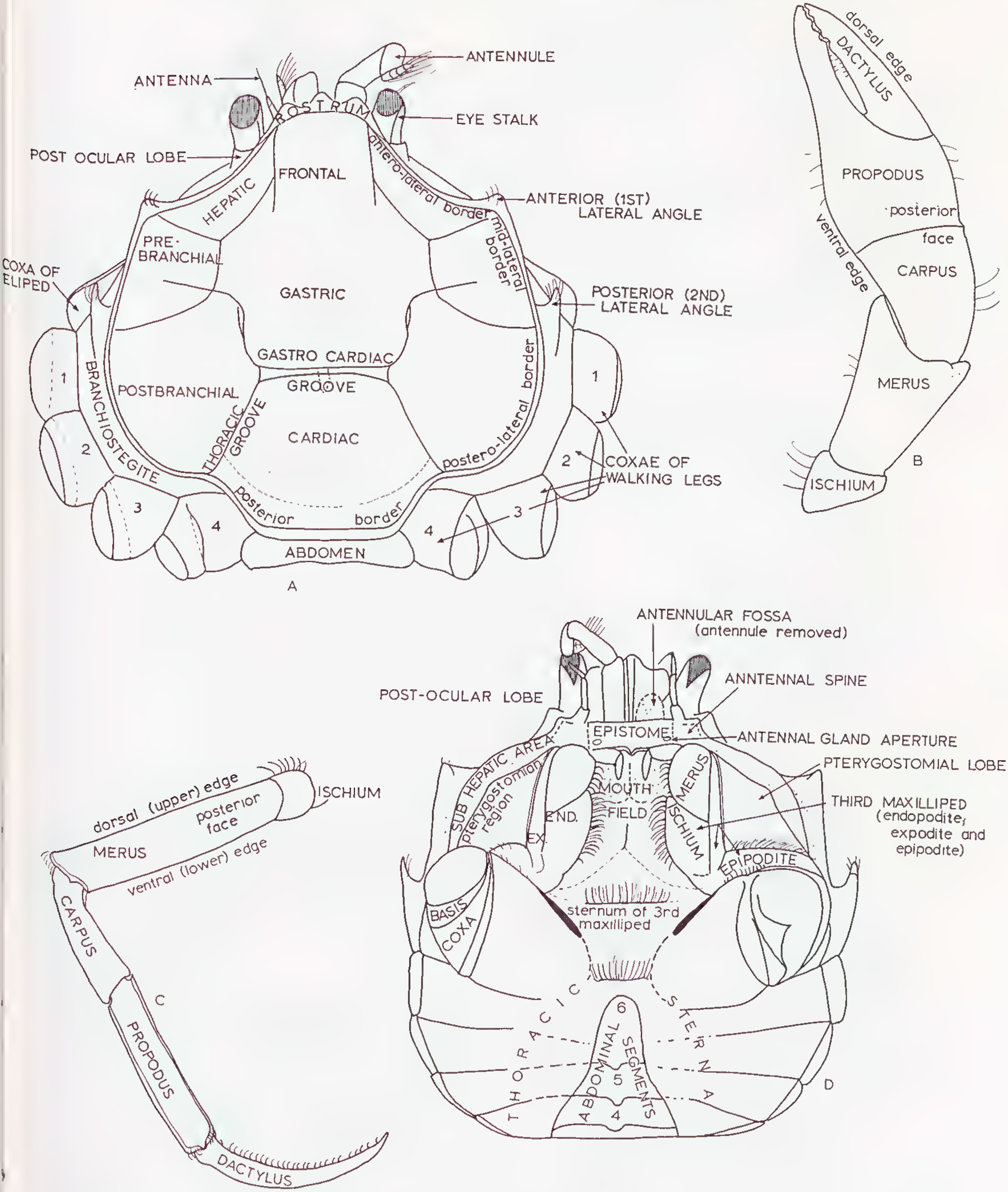

Fig. 1. Generalised hymenosomatid ♂, showing the terms used in descriptions: (A) dorsal view of carapace and leg bases; (B) posterior view of left cheliped; (C) posterior view of 3rd walking leg; (D) ventral view of carapace and leg bases. (From Melrose (1975, Fig. 1) used with permission.)

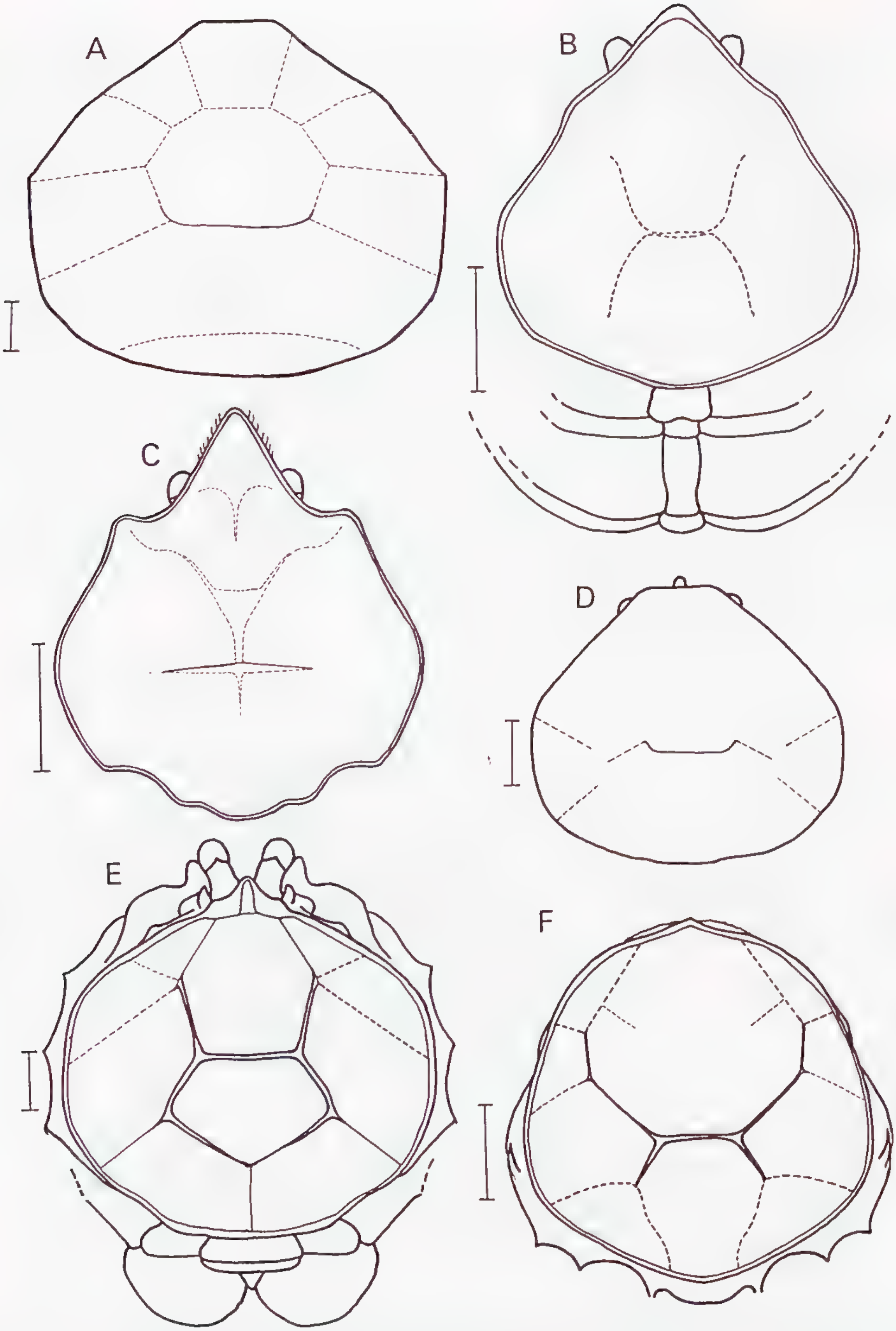

Fig. 2. Dorsal view of carapace, rostrum and eyes (and female abdomen of two species): (A) *Elamena abrolhensis* ♂; (B) *E. gordonae* ♀; (C) *E. umerata* ♀ holotype; (D) *E. truncata* ♂; (E) *Hymenosoma hodgkini* ♀ paratype; (F) *Halicarcinides nuytsi* ♂. Scales =1 mm.

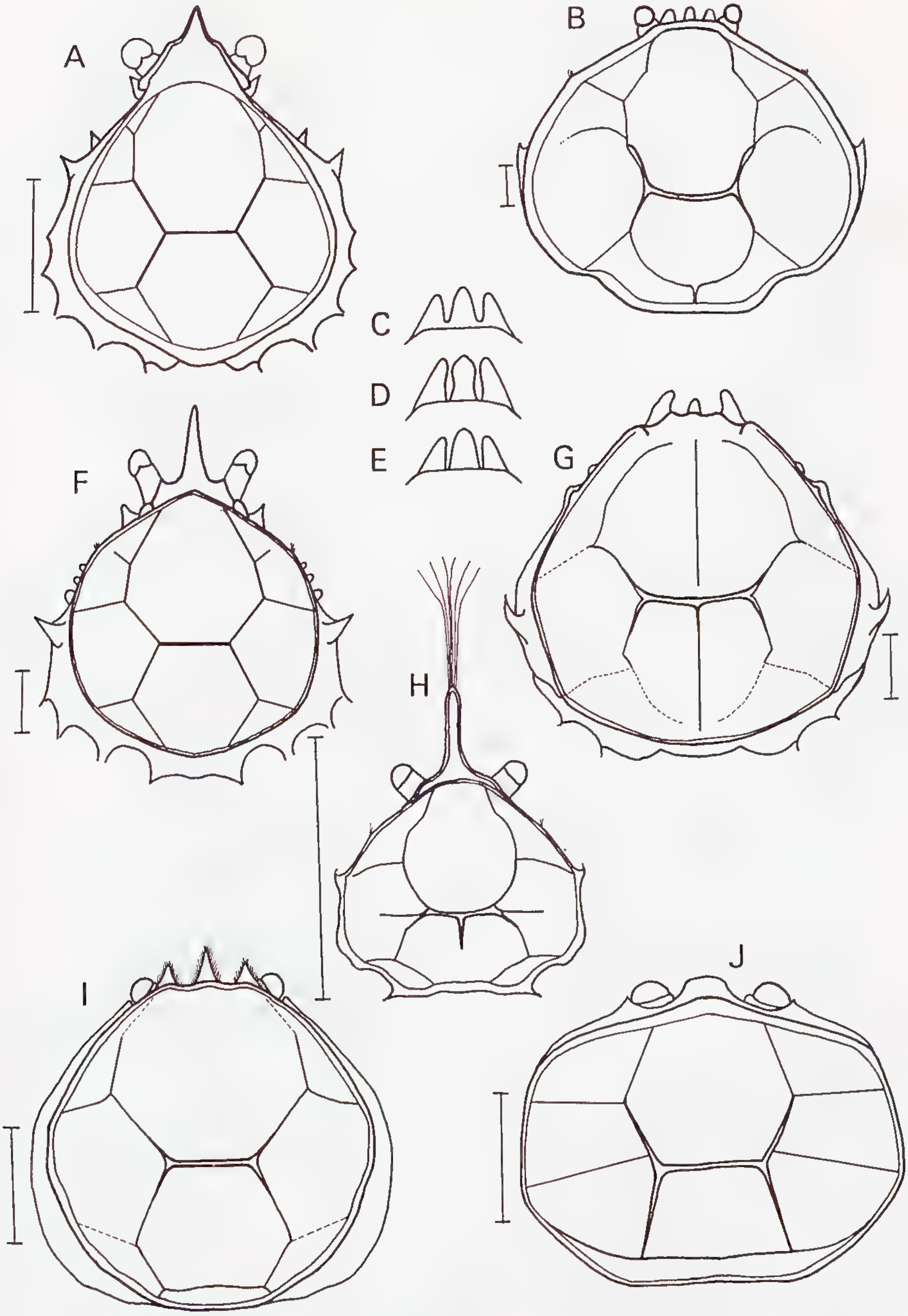

Fig. 3. Dorsal view of carapace, rostrum and eyes: (A) *Halicarcinus bedfordi* ♂; (B) *H. ovatus* ♂; (F) *H. rostratus* ♂; (G) *H. afecundus* ♀ holotype; (H) *H. hondai* ♂; (I) *Elamenopsis aspinifera* ♂ holotype; (J) *E. lineata* ♂. Variation in rostra of *Halicarcinus ovatus*: (C), (D), (E). Scales = 1 mm.

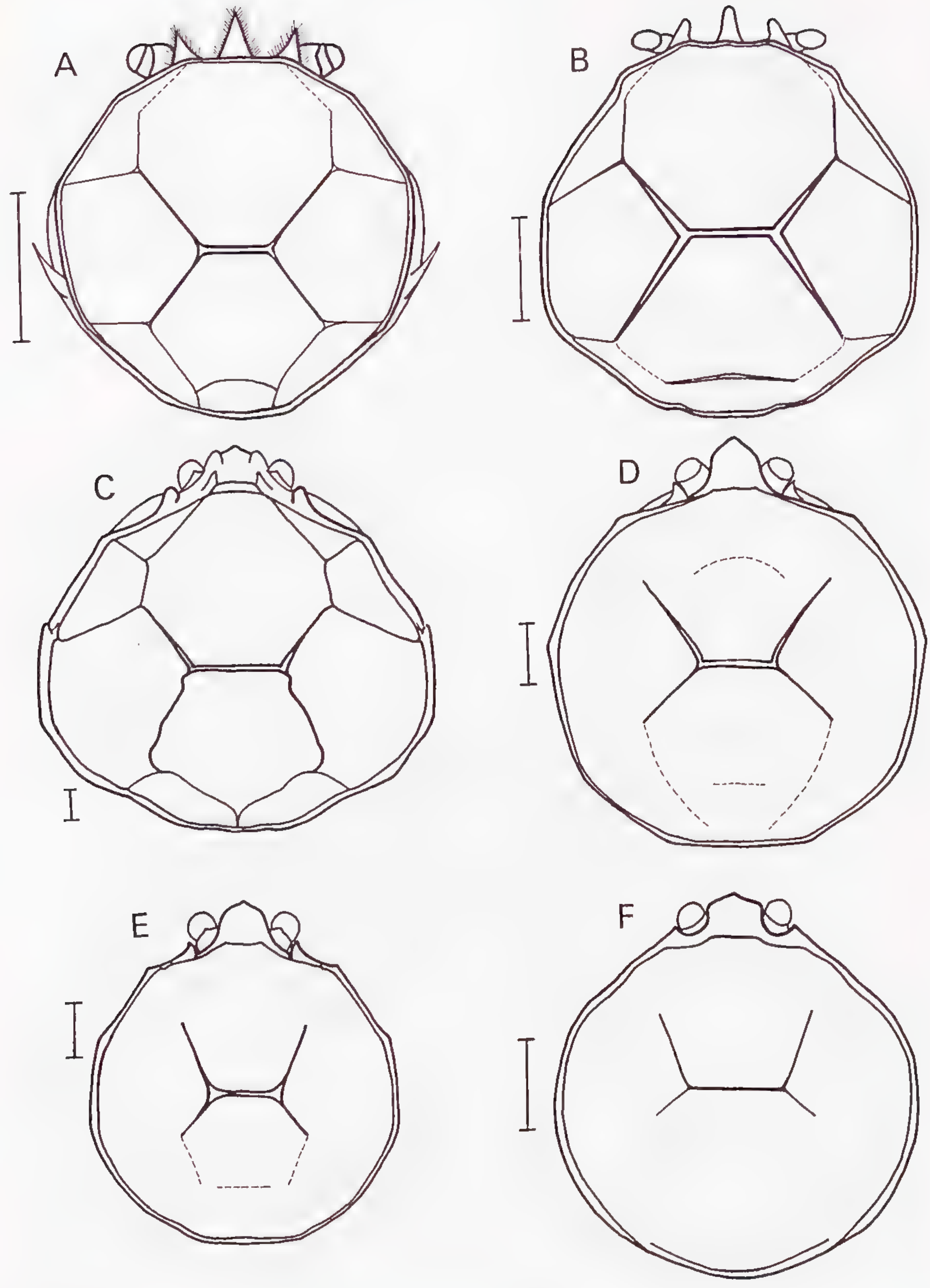

Fig. 4. Dorsal view of carapace, rostrum and eyes: (A) *Elamenopsis octagonalis* ♀ ; (B) *E. torrensica* ♀ holotype; (C) *Amarinus laevis* ♂; (D) *A. lacustris* ♀ ; (E) *A. paralacustris* ♀ ; (F) *A. latinasus* ♀ paratype. Scales = 1 mm.

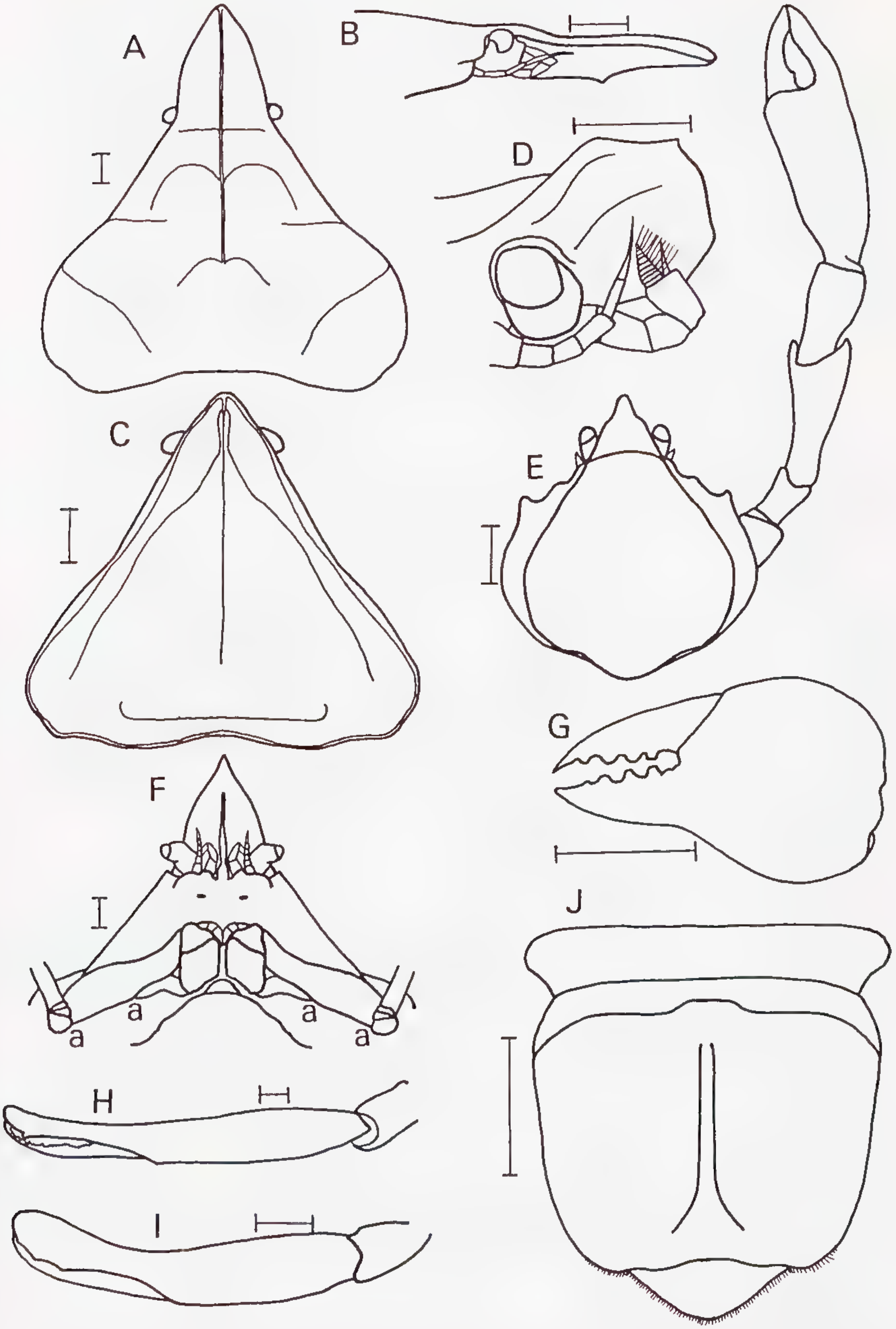

Fig. 5. *Trigonoplax longirostris* ♂: (A) dorsal carapace and eyes; (B) lateral view of rostrum; (F) ventral view of front to show fusion of Milne Edwards apertures (a—a); (H) ventral view of right chela. *T. spathulifera* ♀ holotype: (C) dorsal carapace and eyes; (D) lateral view of rostrum; (I) ventral view of right chela. *Halicarcinus bedfordi* ♂: (E) carapace and right cheliped of large ♂. *Elamenopsis aspinifera* ♂ holotype: (G) lateral view of left chela. *Elamenopsis lineata* ♀ : (J) abdomen. Scales = 1 mm.

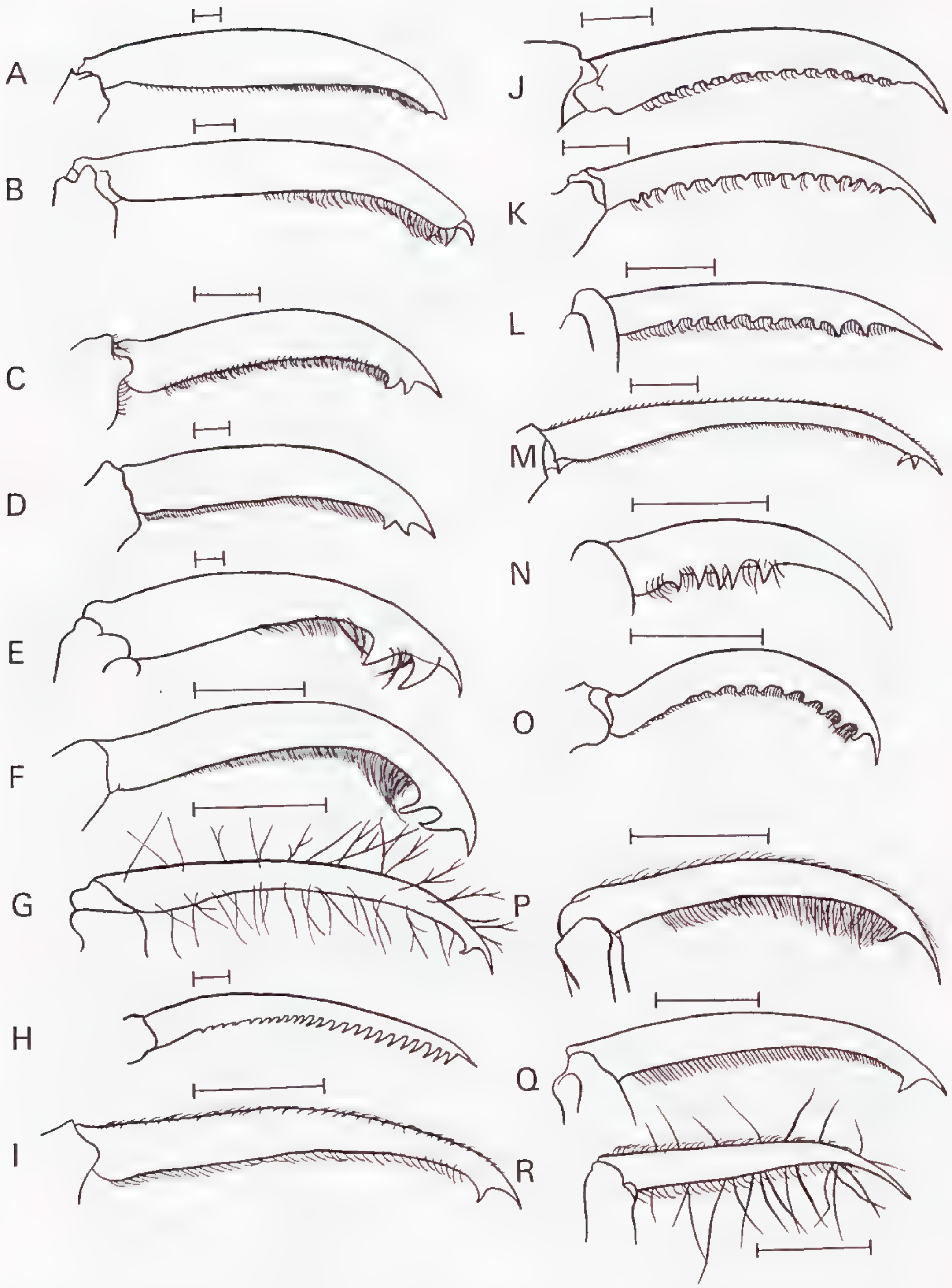

Fig. 6. Dactylus of walking leg: (A) *Trigonoplax longirostris* ♂; (B) *T. spathulifera* ♀ holotype; (C) *Elamena abrolhensis* ♂; *(D) E. truncata* ♂; (E) *E. gordonae* ♀; (F) *E. umerata* ♀ holotype; (G) *Amarinus latinasus* ♀ paratype; (H) *Hymenosoma hodgkini* ♂ paratype; (I) *Halicarcinides nuytsi* ♂; (J) *Halicarcinus ovatus* ♂ (Cockburn Sound); (K) *H. ovatus* ♂ (Port Hacking); (L) *H. rostratus* ♂; (M) *H. afecundus* ♀ holotype; (N) *H. bedfordi* ♂; (O) *H. hondai* ♂; (P) *Elamenopsis octagonalis* ♀; (Q) *E. torrensica* ♀ holotype; (R) *E. aspinifera* ♂ holotype. Scales = 0.5 mm.

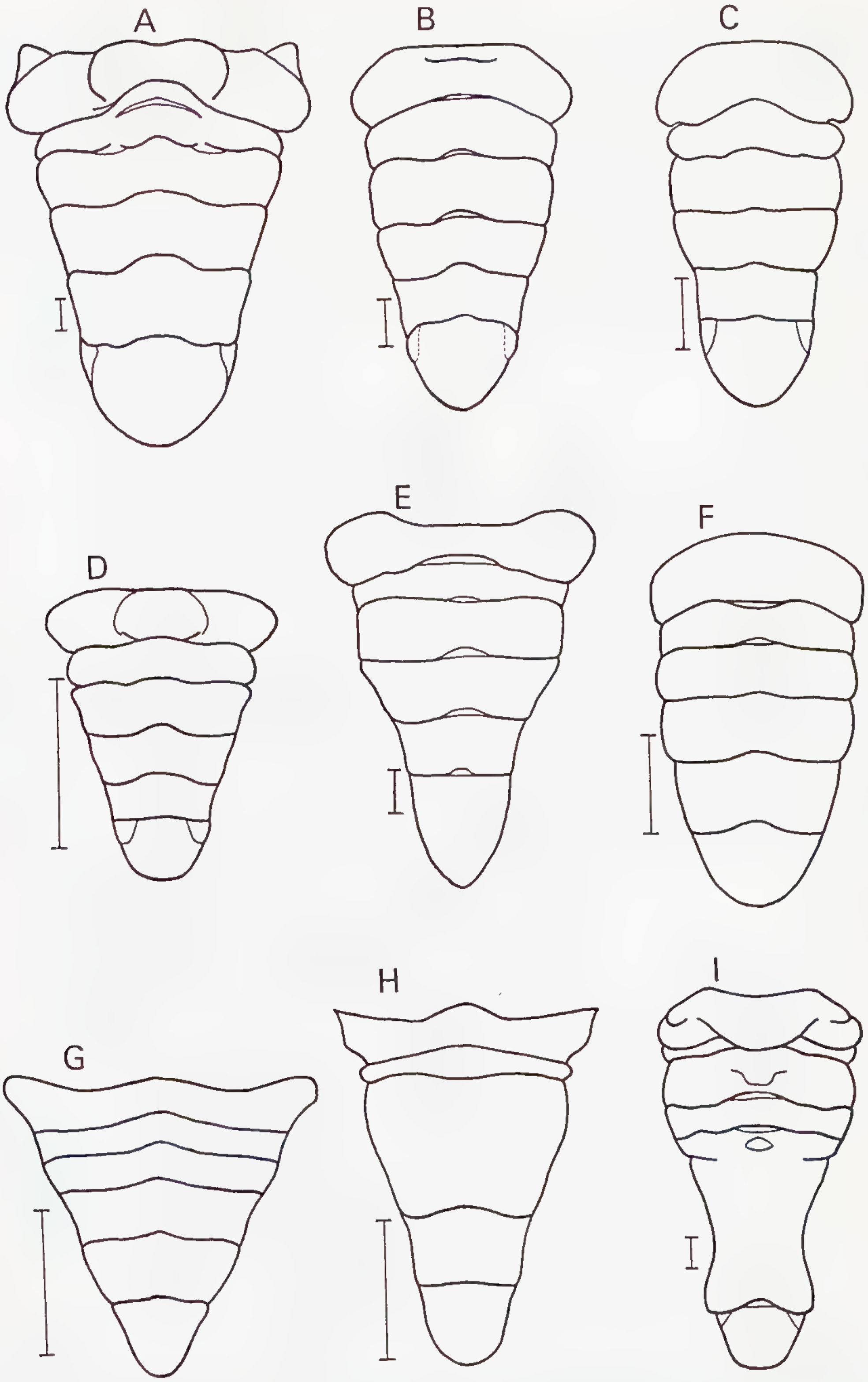

Fig. 7. Male abdomen: (A) *Amarinus laevis;* (B) *A. lacustris;* (C) *A. paralacustris;* (D) *A. latinasus* holotype; (E) *Halicarcinus ovatus;* (F) *H. rostratus;* (G) *H. bedfordi;* (H) *H. hondai;* (I) *Hymenosoma hodgkini* paratype. Scales = 0.5 mm.

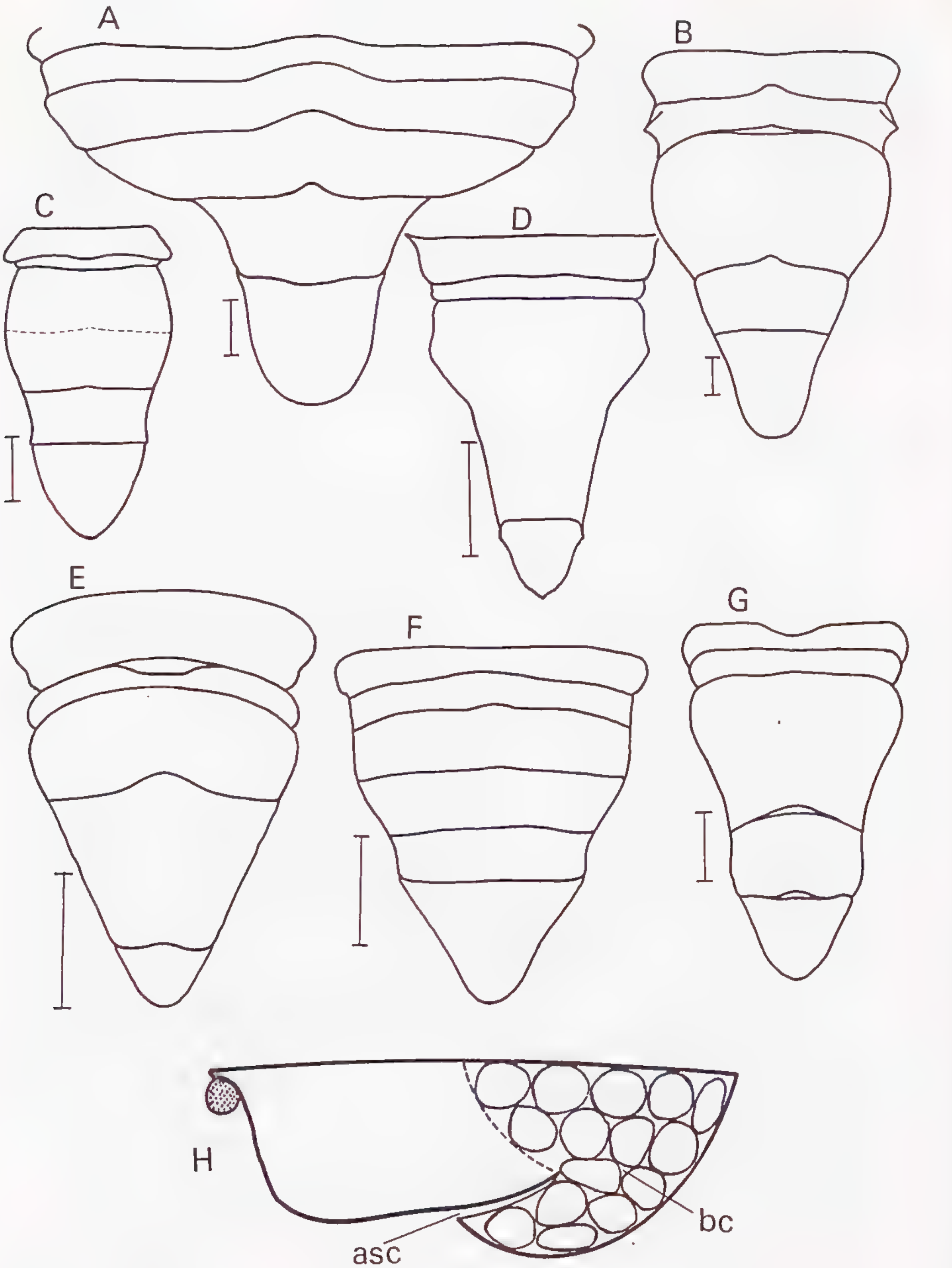

Fig. 8. Male abdomen: (A) *Trigonoplax longirostris;* (B) *Elamena truncata;* (C) *Halicarcinides nuytsi;* (D) *Elamenopsis aspinifera* holotype; (E) *E. lineata;* (F) *Trigonoplax spathulifera* paratype; (G) *Elamena abrolhensis.* Scales = 0.5 mm.

*Elamenopsis* ovigerous ♀: (H) diagrammatic longitudinal section showing the brood cavity and eggs within the cephalothorax and abdomen. asc: abdominosternal cavity (reduced); bc: brood cavity.

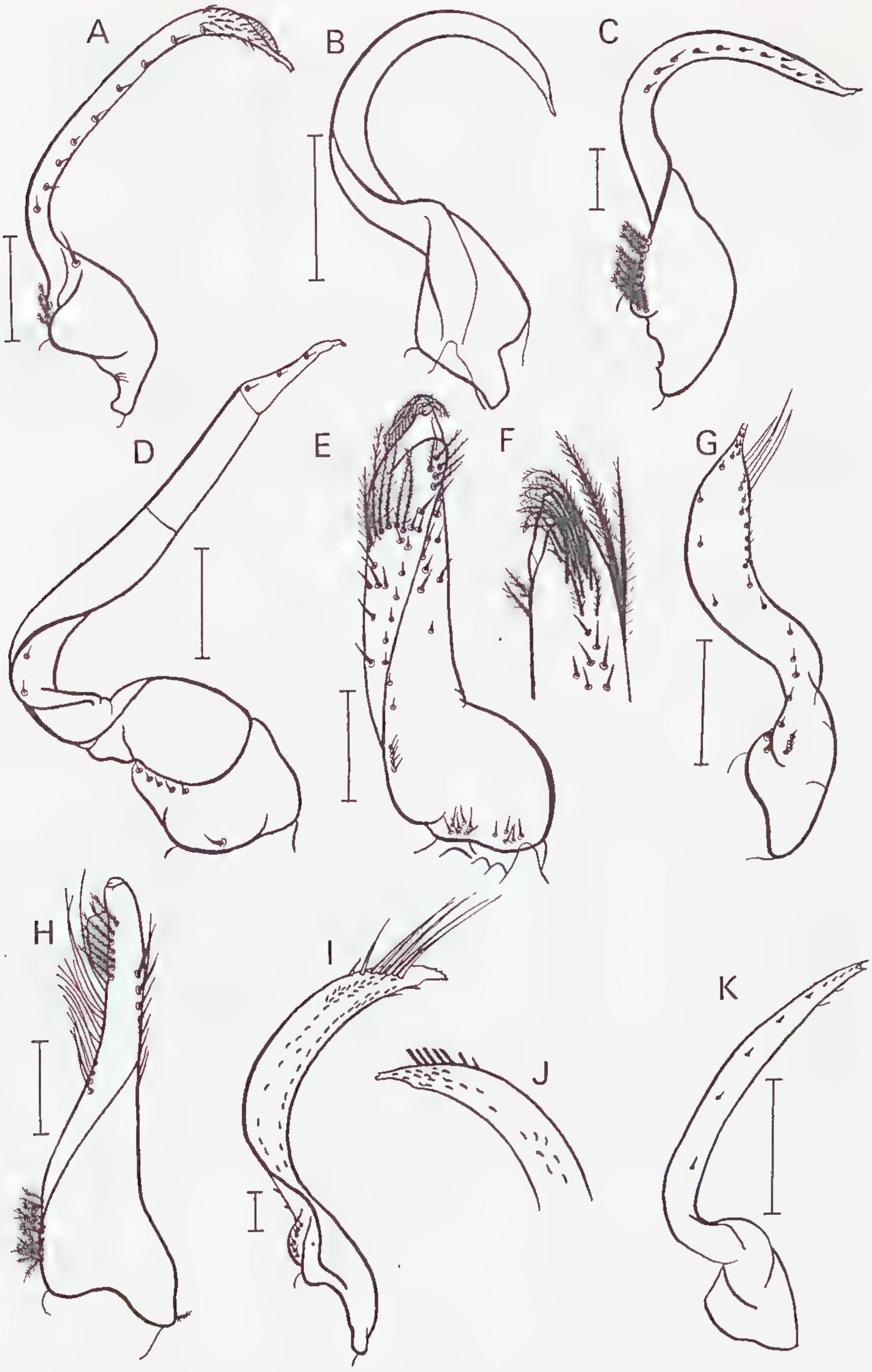

Fig. 9. Male 1st pleopod (lateral view of right side of right pleopod and, for two species, lateral view of left side of apex of right pleopod): (A) *Halicarcinus messor* (Japan); (B) *Elamena umerata* paratype; (C) *Halicarcinus ovatus;* (D) *Halicarcinides nuytsi;* (E) (F) *Halicarcinus bedfordi;* (G) *Trigonoplax spathulifera* paratype; (H) *Halicarcinus rostratus;* (I) (J) *Trigonoplax longirostris;* (K) *Halicarcinus hondai.* Scales = 0.25 mm.

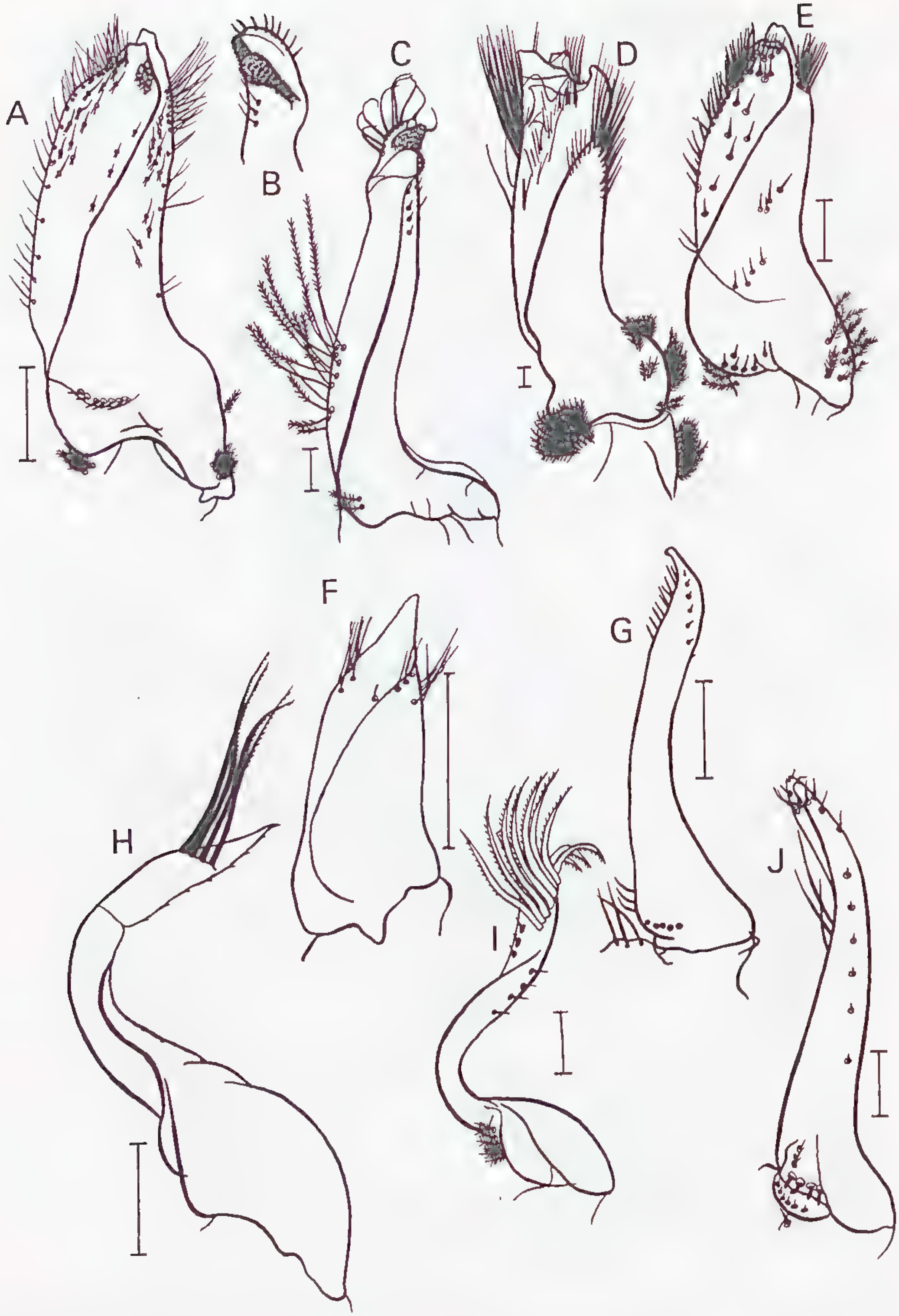

Fig. 10. Male 1st pleopod (lateral view of right side of right pleopod and, for *Hymenosoma hodgkini*, lateral view of left side of apex of right pleopod): (A) *Amarinus paralacustris;* (B) (C) *Hymenosoma hodgkini* paratype; (D) *Amarinus laevis;* (E) *A. lacustris;* (F) *A. latinasus* holotype; (G) *Elamenopsis aspinifera* holotype; (H) *Elamena truncata;* (I) *E. abrolhensis;* (J) *Elamenopsis lineata.* Scales = 0.25 mm.

# AUSTRALIAN GASTROPODS OF THE FAMILY BURSIDAE. PART 1.

## THE FAMILIES OF TONNACEA, THE GENERA OF BURSIDAE, AND REVISION OF SPECIES PREVIOUSLY ASSIGNED TO *TUTUFA* JOUSSEAUME, 1881

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## SUMMARY

In a brief anatomical survey of the Tonnacea, family groups recognised are Tonnidae (subfamilies Tonninae and Oocorythinae), Ficidae, Cassidae (subfamilies Cassinae and Phaliinae), Cymatiidae (subfamilies Cymatiinae, Ranellinae, Distorsioninae) and Bursidae.

In a generic classification of the Bursidae based on opercular, penial, and stomach anatomical features, variceal position is considered to have little taxonomic significance. Genera recognised are *Bursa* Röding, 1798 (with subgenera *Lampadopsis* Jousseaume, 1881; *Bufonariella* Thiele, 1929 [ = *Dulcerana* (Iredale, 1931, unavailable) Oyama, 1964 = *Annaperenna* Iredale, 1936 = *Tritonoranella* Oyama, 1964]; *Colubrellina* Fischer, 1884 ; *Crossata* Jousseaume, 1881 (with (?) subgenus *Olequahia* Stewart, 1926); *Tutufa* Jousseaume, 1881 (with subgenus *Tutufella,* new name for *Lampas* Schumacher, 1817, not of Montfort, 1808); *Bufonaria* Schumacher, 1817 [= *Buffo* Montfort, 1810, not of Lacèpède, 1788, = *Marsupina* Dall, 1904, =*Chasmotheca* Dall, 1904, = *Bursina* Oyama, 1964, = *Gyrineum* of authors, not of Link, 1807] (with subgenus *Aspa* H. and A. Adams, 1853); and *Bechtelia* Emerson and Hertlein, 1964.

The species and subspecies placed in *Tutufa* and its "subgenus" *Tritonoranella* Oyama, 1964 (shown to be a synonym of *Bursa (Bufonariella) are classified as: Bursa (Bufonariella)) latitudo latitudo* Garrard, 1961, Queensland; *B. latitudo natalensis* Coelho & Matthews, 1970, W. Atlantic; *B. latitudo wolfei* n.subsp., Hawaii; *B. (Bufonariella) ranelloides ranelloides* (Reeve, 1844), southern Japan; *B. ranelloides tenuisculpta* Dautzenburg and Fischer, 1906, E. & W. Atlantic to South Africa; *B. ranelloides humilis* n. subsp., Western Australia; *Tutufa (Tutufa) bardeyi* (Jousseaume, 1894), N. Indian Ocean; *T. (Tutufa) bubo* (Linneaus, 1758), Indo-West Pacific; *T. (Tutufa) bufo* (Röding, 1798), Indo-West Pacific; *T. (Tutufella) rubeta* (Linnaeus, 1758), Indo-West Pacific; *T. (Tutufella* n. subgen.) *oyamai* Habe, 1973, E. Indian Ocean and W. Pacific; *T. (Tutufella?) tenuigranosa* (E. A. Smith, 1914), South China Sea; and *T.* aff. *rubeta,* Mocambique. A neotype is designated for *Murex rana* var. *bubo* Linnaeus, 1758, and lectotypes are designated for several other species.

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## INTRODUCTION

Large bursids of the genus *Tutufa* Jousseaume are conspicuous members of the Indo-West Pacific molluscan fauna, and have been recorded in northern New Zealand and around northern Australia from Sydney to Fremantle. The second largest species, *T. bubo* (Linnaeus), is a source of trumpets for the people of the central and southern Indian and Pacific oceans. All but two are relatively common species, but despite detailed investigations by E. A. Smith (1914) and Hedley (1916a) their nomenclature and systematics have troubled all molluscan taxonomists since Linnaeus (1758). Although many recent reviews and shell books have used what is here concluded to be largely correct nomenclature, several species names are stabilised here and all available information brought together on the species of *Tutufa*. Recent examination of the collections and libraries of the Australian Museum, Sydney, the National Museum of Victoria, Melbourne and the Western Australian Museum, Perth, the loan of much tonnacean spirit material by these institutions, the gradual acquisition of a small spirit collection of Tonnacea by the N.Z. Geological Survey, and the loan of two of E.A. Smith's figured specimens of *Tutufa* by the British Museum (Natural History) have enabled me to undertake this initially brief anatomical survey of the Tonnacea and of the Bursidae and *Tutufa* in particular, and to offer my conclusions on the valid species of *Tutufa*.

As an introduction to what is intended to be two papers on the Bursidae of Australia, a brief anatomical survey of the Superfamily Tonnacea is given to differentiate the families, and a classification of the Bursidae is outlined.

## THE FAMILIES OF TONNACEA

### Superfamily **TONNACEA**

This group of large, carnivorous, pseudo-muricacean mesogastropods includes the families Tonnidae, Cassidae, Ficidae, Cymatiidae, and Bursidae. The major shell, opercular, radular and anatomical features of the families are set out here. Important references for opercula, radulae and genera, apart from the writer's personal observations, are Abbott (1968), Turner (1948), Oyama (1964), and Bayer (1971).

Family *Tonnidae:* Shell large, thin, with very inflated last whorl, short siphonal canal, low spire, and sculpture of relatively weak spiral cords only. Outer lip not thickened, or thickened in adult only. Periostracum a thin, smooth sheet. Two subfamilies can be recognised:

Subfamily *Tonninae:* Operculum lacking in adult. Radula with a low, broad central tooth having small interlocking basal processes similar to the relatively larger ones of Bursidae; lateral teeth elongate and massive with large rectangular bases. Jaw plates large. Proboscis extremely large, relatively short and not coiled in the proboscis sheath, but relatively very broad and extremely extendible, with a circular, transversely flattened anterior end. Oesophageal gland represented by glandular area of mid-oesophagus wall, not a discrete sac. Only two accessory salivary glands. Stomach having both digestive gland ducts in a deep pocket in the cardiac arm; the pyloric arm and intestine follow a twice reflected, strongly W-shaped path to the rectum (based on New Zealand specimens of *Tonna variegata cerevesina* Hedley, Fig. 1n). Unfortunately the large and fundamental work on the anatomy of *Tonna* by Weber (1927) has not been available to me, but much of

Weber's information is repeated by Hyman (1967).

Included genera: *Tonna* Brunnich, 1772; *Eudolium* Dall, 1889; *Malea* Valenciennes, 1883, and subgenus *Quimalea* Iredale, 1929.

Subfamily *Oocorythinae:* Operculum present in adult, unique in Tonnacea in being paucispiral with nucleus near adaxial edge of abapical end (see Turner 1948, pl. 75, fig. 8, 9, 11). Radula with central teeth lacking interlocking projections, otherwise similar to that of *Tonna*. Anatomical features not described.

Included genera: *Oocorys* Fischer, 1884, and subgenus *Benthodolium* Verrill and Smith, 1884; *Dalium* Dall, 1889.

Family *Ficidae:* Shell of medium size, thin, with long, narrow pyriform last whorl, long siphonal canal, low spire, and weak spiral sculpture only, although bearing peripheral nodules in some genera; periphery evenly rounded, keeled, or with axial folds. Outer lip not thickened. Periostracum a thin, furry sheet. Operculum absent in *Ficus*, relatively very small, black, and irregularly circular in the only other living genus, *Thalassocyon* (see Beu 1969). Radula with a low, broad, multicuspate central tooth lacking basal interlocking processes, similar to centrals of Oocorythinae and Cymatiidae; lateral teeth relatively large, with long rectangular bases. Jaw plates large. Proboscis exceedingly long and relatively narrow, much coiled in the wide proboscis sheath when not everted. Oesophageal gland a discrete sac. Salivary glands and the two accessory salivary glands relatively solid spongy structures at the rear of the floor of the cephalic cavity. Stomach not seen (based on two incomplete New South Wales specimens of *Ficus filosus* Sowerby).

Ficidae show similarities on the one hand to *Tonna* in the large, enveloping last whorl and dominantly spiral sculpture of the shell and in the absence of an operculum in *Ficus* and, on the other hand, to Distorsioninae in the extremely long narrow proboscis that is much coiled and folded within its wide sheath, in the form of the lateral radular teeth, and in the similarity of the small, black, irregular operculum of *Thalassocyon* to that of *Distorsio*.

Some included genera: *Ficus* Röding, 1798; *Thalassocyon* Barnard, 1960; and the extinct Upper Cretaceous and Tertiary genera *Proficus* Finlay and Marwick, 1937; *Ficopsis* Conrad, 1866; *Trophosycon* Cooper, 1894; *Priscoficus* Conrad, 1866; *Fulguroficus* Sacco, 1890.

Family *Cassidae:* Shell medium to large, moderately to highly inflated, thick and solid, with large last whorl and low spire, short, moderately to very strongly twisted anterior canal, and moderately coarse to very weak spiral and axial sculpture (usually dominantly of relatively weak spiral cords). Outer lip strongly thickened, varices remaining at preadult growth pauses in many genera. Periostracum very weakly developed or absent. Operculum always present. Radula similar to those of Charoniinae and Oocorythinae, but with smaller basal limbs on the lateral teeth. Jaw plates large. Proboscis relatively narrow and short, not coiled in the narrow sheath. Oesophageal gland a discrete sac, usually large and firm, black, lying well to posterior of cephalic cavity. Two large accessory salivary glands present. Stomach a relatively simple, thin-walled tube, intestine straight from stomach to anus. Two subfamilies can be recognised.

Subfamily *Cassinae:* Anterior canal weakly twisted, lacking prominently margined fasciole of Phaliinae; operculum narrowly oval to subrectangular, with nucleus approximately central, or near abapical end; accessory salivary glands firm and of much-folded, broadly tubular structure, lying one behind the other so that the oesophagus is initially central but passes gradually to the right around the left (posterior) accessory salivary gland, and the oesophageal gland is at posterior right (based on *Cassis* [*Hypocassis*] *fimbriata* (Quoy & Gaimard) from Blanche Pt., near Adelaide, South Australia). Shells of most species are relatively elongate and heavily callused, and almost all have more prominent sculpture than those of species in subfamily Phaliinae. *Morum* lacks a radula (Beu, 1976a). Reynell (1905, 1906) has given a good general account of the anatomy of *Galeodea echinophora* (Linnaeus), under the name *Cassidaria rugosa* (*Galeodea* is *not* preoccupied, as frequently supposed, the cited earlier name being spelled *Galeodes*).

Some included genera and subgenera: *Cassis* Scopoli, 1777, and subgenus [*Hypocassis*] *fimbriata* (Quoy & Gaimard) from Blanche Pt., near Adelaide, South 1847; *Sconsia* Gray, 1847; *Morum* Röding, 1798, and subgenera *Herculea* Hanley *in* H. & A. Adams, 1858, and *Oniscidia* Mörch, 1852 (= *Cancellomorum* Emerson and Old, 1963, = *Pulchroniscia* Garrard, 1961); *Galeodea* Link,1807, and subgenus *Galeoocorys* Kuroda & Habe, 1957.

Subfamily *Phaliinae* nov.: shells relatively short and rounded, with weak callusing and usually with weak sculpture, almost entirely spiral; anterior canal very strongly twisted, with a prominently margined fasciole; operculum obtusely fan-shaped, with nucleus at angle between the two straight adaxial edges. Accessory salivary glands thin-walled and sacular, as in Tonnidae, Cymatiidae and Bursidae; salivary glands and accessory salivary glands lateral and clasped on either side of oesophagus well behind proboscis; oesophagus passes down central floor of cephalic cavity so that oesophageal gland is at posterior centre. Stomach a narrow, thin-walled tube with sphincter at anterior end but not at posterior, with finely and closely pleated walls; a prominent typhlosole commences obliquely at the relatively broadly open fold between cardiac and pyloric arms, and gradually reduces in height as it runs along left edge of pyloric arm. Anterior digestive gland duct beneath typhlosole on left edge at bend of stomach, posterior digestive gland duct halfway along left edge of pyloric arm (based on New Zealand specimens of *Semicassis pyrum* (Lamarck)).

Some included genera and subgenera: *Phalium* Link, 1807; *Semicassis* Mörch, 1852 (= *Xenophalium* Iredale, 1927, = *Xenogalea* Iredale, 1927, = *Tylocassis* Woodring, 1928; see Beu, 1976b) and subgenus *Antephalium* Iredale, 1927; *Echinophoria* Sacco, 1890 (= *Mauicassis* Fleming, 1943); *Casmaria* H. & A. Adams, 1853.

Family *Cymatiidae:* shell small to extremely large, thick and solid, varied in shape but generally resembling muricacean neogastropods in most features except that there are only two varices per whorl, rather than three or more; last whorl of most genera relatively small, siphonal canal short to long, spire short to tall; sculpture of most genera of prominent spiral and axial cords and nodules. Outer lip prominently variced in all genera, varices remaining at preadult growth pauses in almost all genera. Periostracum prominent, bearing numerous short to long bristles in most genera. Operculum always present, with central, adaxial, subcentral, or abapically terminal nucleus. Anatomical features varied; only two accessory salivary glands; oesophageal gland a discrete sac; stomach unpleated, with both digestive gland ducts in the pyloric arm, a prominent typhlosole along left edge of pyloric arm, and intestine straight from stomach to anus (in an Australian specimen of *Charonia lampas rubicunda* (Perry); Fig. 1 h). Three subfamilies can be recognised.

Subfamily *Cymatiinae:* Protoconch tall and narrowly conical in almost all genera; periostracum bearing luxuriantly bristled, prominent, thin axial blades; central radular tooth markedly wider than high, with many small, similar denticles on each side of the main cusp; jaw plates large; proboscis relatively short, not coiled within sheath when contracted. These are the Cymatiidae of the tropics, and all have long planktonic larval lives.

Included genera and subgenera: *Cymatium* Röding, 1798; *Ranularia* Schumacher, 1817 and subgenera *Lotoria* Emerson & Old, 1963 and *Gutturnium* Mörch, 1852; *Septa* Perry, 1810 (= *Monoplex* Perry, 1811, = *Cabestanimorpha* Iredale, 1936) and subgenera *Cymatriton* Clench & Turner, 1957, and *Reticutriton* Habe & Kosuge, 1966; *Linatella* Gray, 1857, and subgenus *Gelagna* Schaufuss, 1869.

Subfamily *Ranellinae:* Protoconch low and turbinate; periostracum smooth, furry or with large, evenly spaced bristles, lacking axial blades; central radular tooth approximately equidimensional, with only a few denticles on each side; jaw plates large; proboscis as in Cymatiinae. These are the Cymatiidae of western America, Europe and, above all, the Southern Ocean, with few Indo-West Pacific or Carribbean species. Most have only short planktonic larval lives, and long larval lives are found only in *Ranella olearia, Fusitriton cancellatus, Argobuccinum pustulosum, Charonia,* and presumably *Sassia* (sensu stricto) and *Cabestana (Turritriton) labiosa.*

Included genera and subgenera: *Charonia* Gistel, 1847; *Cabestana* Röding, 1798, and subgenus *Turritriton* Dall, 1904 (= *Tritoniscus* Dall, 1904); *Cymatiella* Iredale, 1929 (= *Vernotriton* Iredale, 1936); *Cymatona* Iredale, 1929; *Sassia* Bellardi, 1873 (= *Phanozesta* Iredale, 1936) and subgenera *Austrosassia* Finlay, 1931, *Austrotriton* Cossmann, 1903 (= *Negyrina* Iredale, 1929) and *Proxicharonia* Powell, 1938; *Haurokoa* Fleming, 1955; *Fusitriton* Cossmann, 1903; *Argobuccinum* Hermannsen, 1846, and subgenera *Mediargo* Terry, 1970 and *Priene* H. & A. Adams, 1858; *Ranella* Lamarck, 1816 (= *Mayena* Iredale, 1917, = *Gyrinopsis* Dall, 1925); *Gyrineum* Link, 1807 (= *Apollon* Montfort, 1810) and subgenus *Biplex* Perry, 1811.

Subfamily *Distorsioninae* Kuroda, Habe & Oyama, 1971 (emend.): protoconch and periostracum as in most Ranellinae, but radula distinctive, with down-curved corners of the broad central tooth, and large lateral teeth resembling those of *Ficus;* jaw plates extremely small; shell very distorted, with prominently plicate inner-lip calluses retained at pre-adult growth pauses; proboscis extremely long and narrow and much folded and coiled in the proboscis sheath when contracted, as in *Ficus*. Lewis (1972) has figured many of the anatomical features of *Distorsio.*

The genitive form of *torsio* (Latin, a wringing or griping) is *torsionis,* so that the subfamily name formed from *Distorsio* should be spelled Distorsioninae.

The single included genus is *Distorsio* Röding, 1798, and its subgenera *Rhysema* Clench and Turner, 1957 (synonymised with *Distorsio* by Lewis, 1972), *Personella* Conrad, 1865, and *Distorsionella* Beu, 1978.

Family *Bursidae:* Shell small to large, extremely thick and solid, similar in shape to Cymatiidae but even more coarsely sculptured; unique anal canal present in outer lip at posterior end of aperture; spire low to moderately tall and siphonal canal short; varices as in Cymatiidae but aligned up sides of spire (as in some genera of Ranellinae) in most genera. Periostracum weakly developed or absent. Operculum always present, with adaxial, abaxial, central, or abapically terminal nucleus. Radula with relatively small, narrow-armed, shallowly ∧-shaped central tooth; near the extremity of each basal arm is a small downward-projecting process (present also in Tonninae) that interlocks adjacent centrals; lateral teeth large, with relatively small, narrow bases and long, strongly hooked cusps. Jaw plates minute in *Tutufa* (s.s.), absent in all other genera and subgenera.

Proboscis relatively short and broad, not folded in sheath when contracted, as in Tonnidae and Cymatiidae, in some genera having a circular, transversely flattened anterior end as in *Tonna*. Oesophageal gland a discrete sac. A third small accessory salivary gland is attached to the right salivary gland. Stomach with one digestive gland duct near posterior end of each arm; path of intestine to rectum straight in most genera examined, but in *Bursa (Bufonariella) granularis* (Röding) it has a small sharp flexure similar to the much larger flexure in *Tonna*. A classification of the family is given below.

### Family **Bursidae:** generic classification

Kuroda, Habe & Oyama (1971, p.133-4) classified the Bursidae of Sagami Bay in two subfamilies, Bursinae (including *"Gyrineum"* = *Bufonaria,* and *Bursa*) and Tutufinae nov. including *Tutufa* and *Bufonariella* [containing *Triton ranelloides* Reeve, 1844, and therefore = *Bursa (Bufonariella)* of this paper] but the only feature *B. (Bufonariella) ranelloides* has in common with *Tutufa* is its variceal position and, as noted below, variceal position is not a useful guide to relationships in the Bursidae. Study of the anatomy, described below, shows that the Bursidae is an extremely homogeneous group in which no subfamilies can be recognised.

Vokes (1973) has offered valuable comments on the classification and taxonomic criteria of the Bursidae, reaching the same conclusion as the writer, that variceal position has little taxonomic significance in Bursidae. Most of her conclusions on relationships agree with those of the writer, but her classification ignores the criteria of the radula, the anatomy and, in particular, the operculum. Her excellent figured Chipola Formation (Lower Miocene) specimen of *Bursa ("Tutufa") pelouatensis* (Cossman and Peyrot) (Vokes 1973, Figs 2a, 6) has close affinities with the recent *B. caelata* (Broderip) and *B. granularis* (Röding), species shown here to belong in *Bursa (Bufonariella)*, which has an abapically terminal opercular nucleus. The figured shell has varices aligned on early spire whorls, becoming unaligned on the last few whorls only, whereas species of *Tutufa* have all varices placed as in cymatiids all down the spire. The resemblance of *B. (Bufonariella) pelouatensis* to *Tutufa (Tutufella) rubeta* is as superficial as are many of the other superficial resemblances in the family cited by Vokes, as *T. rubeta* has an operculum with the nucleus situated near the centre of the height, and a short distance in from the abaxial edge. *B. amphitrites* Maury (Vokes 1973, Fig. 1a, b) also belongs in *Bufonariella*.

Especially characteristic features of the family are the permanent anal siphon in the mantle edge, accommodated in the shell by a deep posterior canal in the outer lip that is produced into the spout which may be short to very long. The accessory salivary glands are very large, and thin-walled. The left salivary gland has attached one long, narrow accessory gland that fills two-thirds of the cephalic cavity, and the right one has attached two smaller accessory glands, the left filling most of the remainder of the cephalic cavity and the right one relatively small and filling the extreme right anterior corner of the cephalic cavity. Prominent processes on each side of the two narrow basal limbs of the central radular teeth interlock all the central teeth. The periostracum is very weakly developed, whereas it is very prominent in the superficially similar Cymatiidae.

According to observed oesophageal, stomach and rectal contents and the report by Houbrick and Fretter (1969, p.424), the prey of Bursidae studied seems to be polychaetes. The extendible proboscis, in many genera with a broad, flat tip and lateral lips, and the large salivary glands are apparently adaptations to anaesthetising tubicolous polychaetes, removing them from their tubes, and swallowing them whole. Many species (in *Bursa* and subgenera) are found on tropical shallow water coral reefs and rocks, and others (in *Tutufa* and *Bufonaria*) are more commonly taken in deeper water on the continental shelf from sand and mud substrates, but habitats vary greatly within one genus.

Genera of the Bursidae have been reviewed only by Jousseaume (1881), Cossman (1903, pp.85-119, in Tritonidae), Dall (1904), Cooke (1916) and Oyama (1964). The latter author regarded almost all recognisable taxa as full genera, and did not consider fossils. As a background setting within which *Tutufa* is treated as a genus and several species previously assigned to *Tutufa* are placed in other genera, a summary is presented here of what the writer considers is a meaningful classification of the Bursidae, expressing relationships in the family as clearly as is possible in Linnaean nomenclature.

### Genus **Bursa** Röding, 1798

*Bursa* Röding, 1798: 128. Type species (by subsequent designation, Jousseaume, 1881, p.174): *Murex bufonius* Gmelin, 1791 (in synonymy of *Bursa monitata* Röding, 1798), Recent, Indo-West Pacific.

*Pseudobursa* Rovereto, 1899: 6. Unnecessary replacement for *Bursa* Röding, 1798.

The designation by Jousseaume (1881, p.174) of *Murex bufonius* Gmelin, 1791, as type species of *Bursa* Röding, 1798 is valid, as Röding (1798, p.128) cited *Murex bufonius* Gmelin as a synonym of his species *Bursa monitata* (International Commission on Zoological Nomenclature, 1964, Article 69(a)i). Recently Beu (1978, p.23) incorrectly attributed the first valid type designation for *Bursa* to Oyama (1964).

Shell small to moderate-sized, dorsoventrally compressed, thick and solid, coarsely sculptured, with short to tall spire; operculum lanceolate, with abapically terminal nucleus. Stomach with the two digestive gland ducts close together near bend between cardiac and pyloric arms. Seminal groove closed.

### Subgenus **Bursa** sensu stricto

Shell small to moderately large for genus, sculptured with large, coarsely rugose, rounded nodules; varices aligned up spire sides; aperture of uniform colour, black or red to white; posterior canal very deep, in most species produced into a long, tubular spine, and spines of previous outer lips remaining prominent on spire.

Some included species: *Bursa (Bursa) bufonia* (Gmelin, 1791) (= *B. luteostoma* Pease, 1861) (Pease 1861, p.397), Indo-West Pacific; *B. (Bursa) mammata* (Röding, 1798) (= *rosa* Perry, 1811, = *siphonata* Reeve, 1844), Indo-West Pacific; *B. (Bursa) tuberosissima* (Reeve, 1844), Indo-West Pacific; *B. (Bursa) xantostoma* (Tapparone-Canefri, 1878) (Tapparone-Canefri 1878, p.249), West Pacific; *Bursa* species with black aperture (Cernohorsky 1967b, p.46, pl. 1, Fig. 2; Reeve 1844b, pl. 5, Fig. 23a).

Almost all male specimens of *Bursa* and its subgenera examined had the seminal groove closed for the whole of its length. The large adult specimen (shell 69 mm high) from Flying Fish Cove, Christmas Island, Indian Ocean (Western Australian Museum, WAM 835-71) dissected in this study (Fig. 1a, 21) had the groove completely closed, as demonstrated by probing and sectioning. The only exception was a small shell with a white aperture, strongly plicate inner lip, long posterior canal spines, and external coarsely rugose sculpture, judged to be a juvenile specimen of *B. bufonia*, from Batangas Province, Luzon, Philippines (Western Australian Museum, WAM 500-69) in which the small narrowly tapering penis bore a clearly open seminal groove. Probe examination under stereoscope enlargement demonstrated that the groove was open for all its length exposed in the mantle cavity. It appears that this specimen (shell 29 mm high) is an immature *B. bufonia* in the early stages of developing its external reproductive system, and that the seminal groove is fully open when first developed, even in genera where it is normally closed when mature.

The stomach of *B. bufonia* (Fig. 1a) has moderately thickened walls, an irregularly plicate, sacular cardiac arm, a straight tubular pyloric arm, both digestive gland ducts near the bend between the two arms, and a typhlosole running from the anterior digestive gland duct into the intestine, more prominent in the intestine than in the stomach.

### Subgenus **Lampadopsis** Jousseaume, 1881

*Lampadopsis* Jousseaume, 1881:175. Type species (by original designation): *Ranella rhodostoma* G. B. Sowerby II, 1841, *ex* Beck MS; Indo-West Pacific.

As the genitive form of *lampas* (Latin, a torch) is *lampadis*, the emendation by Fischer (1884, p.656) of *Lampasopsis* Jousseaume to *Lampadopsis* is justified, and has been followed by most authors.

Shell small to moderate-sized, sculptured with large, rounded nodules that are smooth or bear finely-dissected spiral cords; varices aligned up spire sides; aperture uniformly red to violet, or white with a red parietal blotch; posterior canal extremely short, and shallowly cut into outer lip beyond varix, not into varix.

Some included species: *Bursa (Lampadopsis) rhodostoma* (G. B. Sowerby II, 1841), Indo-West Pacific; *B. (Lampadopsis) venustula* (Reeve, 1844), Polynesia (Cernohorsky 1967a, p.315); *B. (Lampadopsis) cruentata* (G. B. Sowerby II, 1841), Indo-West Pacific; *B. (Lampadopsis) grayana* Dunker, 1863, Red Sea (Dunker 1863-4, p.58, pl. 19, Fig. 5, 6); *B. (Lampadopsis) asperrima* Dunker, 1863, "China" (Dunker, 1863-4, p.57, pl. 19, Fig. 3, 4); *B. (Lampadopsis) thomae* (d'Orbigny, 1842), Caribbean; *B. (Lampadopsis) bergeri* "Sowerby" Tapparone-Canefri, 1881, Mauritius (Tapparone-Canefri 1881, pl. 2, Fig. 1, 2); *B. (Lampadopsis) paulucciana* Tapparone-Canefri, 1876, Mauritius (Tapparone-Canefri 1881, pl. 2, Fig. 16, 17); *B. (Lampadopsis) consobrina* (Mayer, 1871), Upper Miocene of Italy (Bellardi 1873, p.239, pl. 15, Fig. 8), a species closely related to *B. cruentata*.

Specimens identified as *Bursa thomae* (d'Orbigny) sent on loan from the Museum of Comparative Zoology, Harvard University, are identical to Indo-West Pacific specimens of *B. (Lampadopsis) rhodostoma* (Sowerby) in all features, except that they all have a pale pinkish lavender inner lip rather than the pink to deep-red inner lip seen in Indo-West Pacific specimens. As several of the Caribbean shells were collected alive quite recently, this difference cannot be due to fading and is presumed to be significant, and probably *B. thomae* is another example of a Caribbean geographic subspecies of a species otherwise limited to the Indo-West Pacific or Panamic faunas, as so frequently occurs in Tonnacea.

### Subgenus **Bufonariella** Thiele, 1929

*Bufonariella* Thiele, 1929:284. Type species (by monotypy): *Murex scrobilator* Linnaeus, 1758; Pliocene to Recent, Mediterranean.

*Dulcerana* Iredale, 1931:213. Type species (by original designation): *Ranella granifera* Lamarck, 1816 (= *Tritonium granulare* Röding, 1798); Recent, Caribbean and Indo-West Pacific (unavailable, no differentiation from related taxa).

*Annaperenna* Iredale, 1936:310. Type species (by original designation): *Ranella verrucosa* G. B. Sowerby I, 1825; southwest Pacific (Sydney Harbour; Lord Howe Is.; Norfolk

Is.; Kermadec Islands; northern New Zealand).

*Dulcerana* Oyama, 1964:332. Type species (by original designation): *Tritonium granulare* Röding, 1798.

*Tritonoranella* Oyama, 1964:332. Type species (by original designation): *Triton ranelloides* Reeve, 1844, Recent, southern Japan.

Oyama (1964, pp.330, 332) appears to have been the first author to publish the data required to make the name *Dulcerana* available in nomenclature.

Shell of relatively light build, with moderately tall spire, short anterior siphonal canal, posterior canal short and shallow, and sculpture of several rows of small to moderately large, rounded gemmae; varices aligned up spire sides, at least on earliest spire whorls, but either aligned or situated at every ⅔ whorl on last few whorls. Stomach with both digestive gland ducts near bend between cardiac and pyloric arms.

Oyama (1964, p.332) described the operculum of *Bufonariella scrobilator* as having an abaxial nucleus, as in *Tutufa*, and therefore treated *Bufonariella* as a genus related to *Tutufa* and distinct from *Dulcerana* "Iredale" Oyama. However, other authors have described the operculum of *B. scrobilator* as having a terminal, abapical nucleus, and the specimen of *B. scrobilator* figured by Settepassi (1967) bears an operculum with a terminal, abapical, abaxial nucleus. It appears likely that the specimen examined by Cooke (1916) and quoted by Oyama (1964) had an aberrant operculum, as frequently occurs in both Cymatiidae and Bursidae, and as shells referred to *Bufonariella* and *Dulcerana* are extremly similar in all other features the two "subgenera" are here regarded as synonyms.

Oyama (1964, p.332) proposed the genus *Tritonoranella* for *Bursa ranelloides* Reeve, 1844, because its variceal position is like those of *Tutufa* and Cymatiidae, and unlike that of other Bursidae. *Bursa ranelloides* resembles species of *Bursa* (s.str.) rather than species of *Tutufa* in having an abapically terminal opercular nucleus, in having a shallowly embayed base and relatively small interlocking basal processes on the central radular tooth, and in having both digestive-gland ducts situated close together, one on each side of the bend between the cardiac and pyloric arms of the stomach. Also *B.ranelloides* has a light build, tall spire, sculpture of several rows of small to large nodules on spiral cords, a deeply excavated columella, and short, shallow siphonal canals and closely resembles species of *Bursa (Bufonariella)*, especially *B. (Bufonariella) granularis* (Röding). The red-brown parietal colour patch of both species of *Tritonoranella* is seen also in many, although not all, species of *Bursa (Lampadopsis)*, but does not occur in species of *Tutufa*. In short, the only criterion separating *Tritonoranella ranelloides* from *Bursa (Bufonariella)* is the variceal postion, and certainly *Tritonoranella* is related to *Bursa* rather than to *Tutufa*. The two closely related species *B. ranelloides* (Reeve) and *B. latitudo* Garrard, revised below, are the only species sharing widely spaced varices, and as variceal postion is variable in a few species of *Bursa (Bufonariella)*, the differences between *Tritonoranella* and *Bufonariella* do not seem sufficient bases for a subgenus, and the name *Tritonoranella* Oyama, 1964 is here regarded as a synonym of *Bufonariella* Thiele, 1929.

Iredale (1936, p.310) proposed *Annaperenna* for the single species *Bursa verrucosa* G. B. Sowerby I, 1825. *Bursa verrucosa* resembles coarsely sculptured Japanese specimens of *B. (Bufonariella) ranelloides ranelloides* (Reeve) closely in shape, sculpture, smoothness of surface between nodules, aperture shape and sculpture, and presence of a red parietal area, and differs from *B. ranelloides* only in its rows of larger nodules below the peripheral one, the external surface colouration, and in having all its varices aligned up the sides of the spire. Powell (1967, p.190, fig. 3) described the operculum as "irregularly ovate with a subterminal nucleus", and figured a radula with a deeply embayed central tooth, bearing a relatively short main cusp and small interlocking basal processes similar to those of *Bursa bufonia*. There can be little doubt that *Bursa verrucosa* belongs in *B (Bufonariella)* near *B. ranelloides*, and the name *Annaperenna* Iredale, 1936 is therefore regarded as synonym of *Bufonariella* Thiele, 1929.

Species placed in the subgenus *Bufonariella* differ from *Bursa* (s.str.) in their markedly more cymatiid-like appearance, brought about by a thinner and more finely sculptured shell and a markedly taller spire than in species of *Bursa (Bursa)* or *Lampadopsis*.

Some included species are: *Bursa (Bufonariella) granularis* (Röding, 1798) (= *rubicola* Perry, 1811, = *granifera* Lamark, 1816, = *semigranosa* Lamarck, 1816, = *kowiensis* Turton, 1932, = *cumingiana* Dunker, 1864 [Dunker 1863-4, p.59, pl.19, fig. 7,8]= *affinis* Broderip, 1833, = *cubaniana* d'Orbigny, 1842, = *livida* Reeve, 1844), Indo-Pacific and Caribbean; *B. (Bufonariella) coriacea* (Reeve, 1844), locality?; *B. (Bufonariella) fijiensis* (Watson, 1880), Fiji; *B. (Bufonariella) corrugata* (Perry, 1811) (= *caelata* Broderip, 1833, = *ponderosa* Reeve,1844, = *louisa* M. Smith, 1948), Caribbean and central Western America; *B. (Bufonariella) calcipicta* (Dall, 1908) (see Keen 1971, fig.965), Panamic; *B. (Bufonariella) pustulosa* (Reeve, 1844), West Africa and Ascension I.; *B. (Bufonariella) dunkeri* Kira, 1961 (Kira 1961, p.54, pl.21, fig. 18; *nomen nudum* in earlier editions), Japan; *B. (Bufonariella) verrucosa* (G. B. Sowerby I, 1825) (= papilla Wood, 1828), southwest Pacific; *B. (Bufonariella) scrobilator* (Linnaeus, 1758), Mediteranean; *B (Bufonariella) latitudo* Garrard, 1961, with subspecies (revised below) *B. latitudo latitudo*, Queensland, *B. latitudo natalensis* Coelho & Matthews, 1970, western Atlantic, and *B. latitudo wolfei* n. subsp., Hawaii; *B (Bufonariella) ranelloides* (Reeve, 1844), with subspecies (revised below) *B. ranelloides ranelloides*, southern Japan, *B. ranelloides tenuisculpta* Dautzenburg & Fischer, 1906, Atlantic and South Africa, and *B. ranelloides humilis* n. subsp., Western Australia; and *B (Bufonariella) rehderi* Beu, 1978, Philippine Islands (Beu, 1978).

European Miocene species include *B. (Bufonariella) grateloupi* (d'Orbigny, 1842) (see Cossmann and Peyrot 1923, pl. 15, fig. 42, 43); *B. (Bufonariella) nodosa* (Borson, 1821) (Bellardi 1873, pl 15, fig. 5) and var. *subgranifer* (d'Orbigny, 1842) (Cossmann and Peyrot 1923, p.307, pl. 16, fig. 28, 29); *B. (Bufonariella) pelouatensis* (Cossmann and Peyrot, 1923) (Cossmann and Peyrot 1923, pl. 15, fig. 38, 39); *B. (Bufonariella) inaequicrenata* (Cossmann and Peyrot, 1923) (Cossmann and Peyrot 1923, pl. 15, fig. 44, 45); *B. (Bufonariella) lessonae* (Bellardi, 1873) (Bellardi 1873, pl.15, fig. 10) and var. *occidentalis* (Cossmann and Peyrot, 1923) (Cossmann and Peyrot 1923, pl.16, fig. 16, 17); *B. (Bufonariella) tuberosa* (Borson, 1821) (Bellardi 1873, pl.15, fig. 7); and *B. (Bufonariella) austriaca* (Hörnes and Auinger, 1884) (Bosch *et al.* 1975, pl.13, fig. 2), a species closely related to but shorter than the living *B. scrobilator*.

### *Subgenus* **Colubrellina** Fischer, 1884

*Colubrellina* Fischer, 1884:656. Type species (by original designation): *Ranella candisata* Lamarck, 1816 (= *Murex conditus* Gmelin, 1791), Recent, Indo-West Pacific.

Posterior canal very short, shallow; spire extremely tall, so that shell resembles *Colubraria;* varices aligned up spire sides; sculpture of many rows of similar fine, sharp granules.

Several recent workers have regarded *Colubrellina* as a full genus, and some have ranked *Bufonariella* (= *Dulcerana*) as a subgenus of it. Oyama (1964, pl.332) included

*Colubrellina* in his key in genera with "almost terminal (anteriormost) nucleus" in the operculum, so that *Colubrellina* evidently also is closely related to *Bursa (s.s.) and Bufonariella,* and here is regarded as a subgenus of *Bursa*.

The subgenus includes only the uncommon Indo-West Pacific *Bursa (Colubrellina) condita* (Gmelin), recently discussed and figured by Cernohorsky (1972, p.200, fig.12). Specimens of *B. condita* in the Australian Museum are from Tryon I., Capricorn Group, southern Great Barrier Reef, Queensland (C.81612).

### Genus **Crossata** Jousseaume, 1881

*Crossata* Jousseaume, 1881:175. Type species (by original designation): *Ranella ventricosa* Broderip, 1833, Recent, central Western America.

Varices low and weak, almost aligned up spire sides; posterior canals very short and broadly open; shell large, relatively thin, sculptured with large nodules; operculum as in *Bursa*. Radula (Cooke, 1916, p.10, figs.3, 6) with unusually low and broad central tooth bearing only a single large cusp.

Included species are *Crossata ventricosa* (Broderip, 1833), (= *tenuis* Potiez & Michaud, 1838), Recent, Panamic province; *C. californica* (Hinds, 1843), Recent, California; and *C. sonorana* (Berry, 1960) (see Keen, 1971, p.509, fig. 967).

### ?Subgenus **Olequahia** Stewart, 1926

*Olequahia* Stewart, 1926:382. Type species (by original designation): *Cassidaria washingtoniana* Weaver, 1912, Eocene, western North America.

Some figures of *Olequahia washingtoniana* resemble *Bufonaria* (e.g., Wenz 1940, fig. 3063; Weaver, 1942, pl.84, fig. 6) but others (e.g., Weaver 1942, pl. 84, fig. 10, 11) closely resemble *Crossata* in their low form, sculpture of weak, widely spaced cords, and broadly open posterior canal. Certainly the broad form, unusual fine, low, widely spaced spiral sculpture, and broadly open posterior canal give *Crossata* a highly distinctive appearance and suggest that it has had a long Tertiary history in Western America. Probably *Olequahia* was ancestral to *Crossata*, and in view of their similarity it seems best at present to treat *Olequahia* as a subgenus of *Crossata*.

### Genus **Tutufa** Jousseaume, 1881

*Tutufa* Jousseaume, 1881:175. Type species: *Murex rana bubo* Linnaeus, 1758 (ICZN Opinion 1074); Recent, Indo-West Pacific.

Shell moderate-sized to extremely large, including the largest Bursidae; posterior and anterior canals very short, spire moderately tall; varices situated at every ⅔ whorl, i.e. every 240° around spire; operculum with nucleus at or slightly below half height and slightly towards the centre from the abaxial margin; head-foot maculated with red or dark brown.

### Subgenus **Tutufa** sensu stricto

Shell very large; columella weakly plicate or smooth; seminal groove open; cephalic tentacles not bearing colour rings; stomach (of *T. bufo)* has typhlosoles both in front of and behind digestive gland ducts.

Included species (revised below): *Tutufa (Tutufa) bardeyi* (Jousseaume, 1894), northern Indian Ocean; *T. (Tutufa) bubo* (Linnaeus, 1758), Indo-West Pacific; *T. (Tutufa) bufo* (Röding, 1798), Indo-West Pacific.

### Subgenus **Tutufella,** new name

*Lampas* Schumacher, 1817:252. Type species (by monotypy): *Lampas hians* Schumacher, 1817 (refers to Martini, 1780, vol.4, pl.128, figs. 1236-7) = *Murex rana* var. *rubeta* Linnaeus, 1758; Recent, Indo-West Pacific (not *Lampas* Montfort, 1808, Foraminiferida).

The new name *Tutufella* is here proposed as a replacement name for the preoccupied *Lampas* Schumacher, 1817, not of Montfort, 1808, and takes the same type species.

Shell medium-sized to moderately large; columella closely plicate; seminal groove closed; cephalic tentacles with two dark colour rings; stomach with typhlosole behind digestive gland ducts only.

Inlcuded species (revised below) are: *Tutufa (Tutufella) oyamai* Habe, 1973, West Pacific; *T. (Tutufella) rubeta* (Linnaeus, 1758), Indo-West Pacific; *Tutufa (Tutufella?) tenuigranosa* (E. A. Smith, 1914), South China Sea; and *T.* n.sp.? aff. *rubeta* (Röding), Moçambique.

### Genus **Bufonaria** Schumacher, 1817

*Buffo* Montfort, 1810:575. Type species (by monotypy): *Buffo spadiceus* Montfort, 1810 (= *Murex bufo* Bruguière, 1792), Recent, Caribbean (not *Buffo* Lacépède, 1788, Vertebrata).

*Bufonaria* Schumacher, 1817:251. Type species (by subsequent designation, Herrmannsen, 1846, p.135): "*Ranella spinosa* Lamck" = *Bufonaria spinosa* Schumacher, 1817 (refers to Martini, 1780, vol. 4, pl. 133, fig. 1274-1276) = *Gyrineum echinatum* Link, 1807; Recent, Indo-West Pacific.

*Marsupina* Dall, 1904:118 (new name for *Buffo* Montfort, 1810, not of Lacépède, 1788).

*Chasmotheca* Dall, 1904:118. Type species (by original designation): *Ranella foliata* Broderip, 1833, Indo-West Pacific.

*Bursina* Oyama, 1964:333. Type species (by original designation): *Ranella nobilis* Reeve, 1844, West Pacific.

This is "*Gyrineum* Link, 1807" of many authors, but not of Link, 1807. The type designation for *Gyrineum* given by Rovereto (1899) is invalid as the designated species, *Ranella spinosa* Lamarck, was not expressely included by Link. The next type designation for *Gyrineum* is that by Dall (1904, p.131), who cited *Murex gyrinus* Linnaeus, 1758 as the type species, and in the same work (p.115) clearly stated that *Gyrineum verrucosum* Link, 1807 is a synonym of *Murex gyrinus* Linnaeus, thereby making *Gyrineum verrucosum* Link the type species of *Gyrineum* Link, 1807, under the Code (Article 69 (a) (vi)). Therefore *Gyrineum* Link, 1807, must be used as a senior synonym of *Apollon* Montfort, 1810 (Cymatiidae), as it has by many recent writers, and the next available name, *Bufonaria* Schumacher, used in its place in Bursidae.

Vokes (1973, p.100) has pointed out that the name *Murex bufo* Bruguière, 1792 (Reference: Actes Soc. H.N. Paris, 1 (1): 126; Sherborn 1902, p.147) is an earlier name for

*Bufonaria spadicea* (Montfort, 1810). To workers who place all Bursidae in *Bursa*, whether subgenera are used or not, *Tutufa bufo* (Röding, 1798) will be a secondary homonym of *Bufonaria bufo* (Bruguière, 1792), and the species of *Tutufa* must be called *Bursa (Tutufa) lissostoma* (E. A. Smith, 1914), the only synonym proposed for the species. However, when the names are placed in the separate genera *Bufonaria* and *Tutufa*, as is strongly urged here, the secondary homonyms *B. bufo* (Bruguière) and *T. bufo* (Röding) should be retained (International Commission on Zoological Nomenclature, 1964, Article 59 (c)).

### Subgenus **Bufonaria** sensu stricto

Varices aligned up spire sides, at least on early part of spire; posterior canals short to very long, when long aligned up previous varices on spire; shell dorsoventrally compressed, light in weight, sculptured with numerous rows of small granules and, in some species, with nodules or spines at the shoulders of the varices. Seminal groove open. Operculum fan-shaped with nucleus in centre of adaxial margin, as in Cassidae subfamily Phaliinae, to subcentral near adaxial margin, to almost central (in *B. nobilis*).

A wide range of shape, degree of spination of the varices, and amount of sculpture of the inner-lip shield is here included in *Bufonaria* s.s., but all types intergrade and there are no anatomical or opercular differences between the synonymised taxa, except as noted below for *Bursina* Oyama. The variceal and siphonal features used by Dall (1904, p.118) and Oyama (1964) to distinguish such "genera" as *Marsupina* and *Chasmotheca* from *Bufonaria* are considered to be specific characters only.

Oyama (1964, p.333) separated *"Bursina" nobilis* from *Bufonaria* because its operculum has a central rather than an adaxial nucleus. A live-collected specimen of *Bufonaria nobilis* (Reeve) in the Western Australian Museum (Mariel King Memorial "Pele" expedition, Sta. AHI/5, near Tg. Bt. Kapal, Haruku Islands, east of Ambon, Moluccas, 3°36′S, 128°24′E, 31 May 1970, 45-48 fms; WAM 616-74) has a damaged, elongated operculum, similar in shape to those of *B. rana* and other typical species of *Bufonaria*, but with the nucleus slighly off-centre near the adaxial margin, rather than hard against the adaxial margin. The close similarity of the shell of *B. nobilis* to those of other species here included in *Bufonaria* (s.s.) and the similarity of opercular shape to those of *Bufonaria* suggest that *"Bursina" nobilis* belongs in *Bufonaria* (s. str.) A large suite of *Bufonaria margaritula* (Deshayes *in* Boulenger, 1832) from Tayabus Bay, W. Quezon Province, Luzon, Philippines (J. E. Norton Colln., Western Australian Museum, WAM678-70) shows that this species is similar to *B. nobilis* in its angular shape, with sharp nodes on the varices at the peripheral and basal angulations differing from *B. nobilis* in its much shorter form, especially the shorter spire. The opercula of shells in the suite are all unusually broadly oval for species of *Bufonaria*, and consistently have their nuclei a short distance in from the centre of the adaxial margin, half-way between the position in *B. nobilis* and that in more common species of *Bufonaria* such as *B. rana*. It appears that the position of the opercular nucleus in *Bufonaria* depends on the angle of the parietal area to the columella, as tall-spired species with almost straight inner lips, such as *B. nobilis*, have the opercular nucleus furthest from the columella, short-spired cassid-shaped species with the columella at a marked angle to the parietal area have the opercular nucleus against the columella, and the position is intermediate in species of intermediate shape. Therefore a varied opercular nucleus position is accepted in *Bufonaria*, and *B. nobilis* is regarded as a species of *Bufonaria* (sensu stricto). The name *Bursina* Oyama, 1964 is synonymised with *Bufonaria* Schumacher, 1817.

Some included species: *Bufonaria (Bufonaria) nobilis* (Reeve, 1844); *B. (Bufonaria) echinata* (Link, 1807) (= *spinosa* Lamarck, 1816, = *suensonii* Mörch, 1852); *B.*

*crumenoides* (Valenciennes, 1832) (Valenciennes 1832, p.297) (= *crumena* of authors, not of Lamarck); *B. elegans* (G. B. Sowerby 2nd *ex* Beck MS, 1835); *B. foliata* (Broderip, 1833); *B. koperbergae* (Altena, 1942), Pliocene of Java & Timor, Recent in "Siboga" stns. 12 & 306 (Altena 1942, p.109, fig.4, a, b, 5); *B margaritula* (Deshayes, 1832) (= *neglecta* G. B. Sowerby 2nd 1835); *B. rana* (Linnaeus, 1758) (= *albivaricosa* Reeve, 1844, = *crumena* Lamarck, 1816, not *crumena* of authors); *B. subgranosa* (G. B. Sowerby 2nd, *ex* Beck MS, 1835); *B. pacator* (Iredale, 1931) (?= *margaritula* Deshayes), all Indo-West Pacific; *B. gnorima* (Melville, 1918), northern Indian Ocean (Melville 1918, p.138, pl. 4, fig. 1); *B fernandesi* Beu, 1977, Moçambique (Beu 1977); and *B. bufo* (Bruguière, 1792) (= *spadicea* Montfort, 1810, = *crassa* Dillwyn, 1816, = *granulata* Lamarck, 1816), Caribbean. Several of the Indo-West Pacific species were recorded from the Miocene of Java by Martin (1899).

### Subgenus **Aspa** H. and A. Adams, 1853

*Aspa* H. and A Adams, 1853: 106. Type species (by monotypy): *Ranella laevigata* Lamarck, 1816 (= *Murex marginatus* Gmelin, 1791), Miocene to Pleistocene, Europe; Recent, Mediterranean.

Spire very low; varices low and rounded, resembling those of *Argobuccinum* (sensu stricto); shell squat, rounded, finely sculptured; operculum and other features as in *Bufonaria* sensu stricto.

The included species comprise only the Recent Mediterranean *Bufonaria (Aspa) marginata* (Gmelin) and a lineage of ancestral species in the Tertiary and Quaternary rocks of Europe, perhaps all part of the variation of *B. (Aspa) marginata: B. (Aspa) subgranulata* (d'Orbigny, 1842) (Cossmann and Peyrot 1923, p. 313, pl. 15, fig. 54; pl. 17, fig. 7); *B. (Aspa) depressa (*Grateloup, 1840) (Cossmann and Peyrot, 1923, p. 316, fig. 1, 2; pl. 17, fig. 8, 9).

### Genus **Bechtelia** Emerson and Hertlein, 1964

*Bechtelia* Emerson and Hertlein, 1964: 360. Type species (by original designation): *Gyrineum strongi* Jordon, 1936, Pleistocene, Baja, California.

Figures of the type species of *Bechtelia* by Emerson and Hertlein (1964, fig. 59) and Durham (1950, pl. 29, fig. 19, 22) and a plaster cast of the holotype of *Gyrineum strongi* kindly presented by the late Dr Leo Hertlein show that *Bechtelia strongi* has a short, narrow, constricted posterior siphonal canal, a prominently dentate aperture unlike that of any Cymatiidae, and the varices aligned up the spire sides, and thus belongs in the Bursidae. It is perhaps related to *"Marsupina" nana* (Broderip and Sowerby, 1829) of the Recent Panamic Fauna. *Bufonaria nana* is far from a typical species of *Bufonaria* with its almost smooth shell surface, but the posterior canals of *B. nana* are deep and extend well up the spire, so it may not be related to *Bechtelia strongi*. At present *Bechtelia* appears to be an endemic monotypic, Panamic Pleistocene genus.

## SPECIES REFERRED TO *TUTUFA*

### Genus **Tutufa** Jousseaume, 1881

The status of type-species designations where the designated name refers to more than one valid taxon is not covered by the Code. Jousseaume (1881) designated *Murex lampas* Linnaeus, 1758 as type species of *Tutufa* but strictly speaking this is a species of *Charonia*, by designation by Beu (1970, p. 211). Jousseaume presumably intended to designate as type the large bursid generally known as *Bursa* (or *Ranella*) *lampas* until about 1920, and now usually called either *Bursa* (or *Tutufa*) *gigantea* E. A. Smith or *B. bubo* (Linnaeus). Beu (1973) applied to the International Commission on Zoological Nomenclature to designate *Murex rana* var. *rubeta* Linnaeus, 1758 as type species of *Tutufa,* on the grounds that it was the most commonly used name in the complex, but subsequently Rehder (1974) modified this to an application to designate *Murex rana* var. *bubo* Linnaeus, 1758 as type species. The International Commission on Zoological Nomenclature (1977) designated *Murex rana bubo* Linnaeus, 1758 as type species of *Tutufa* Jousseaume in Opinion 1074.

*Tutufa* is a distinctive genus of Bursidae characterised, as is noted above, by its moderate to extremely large size; by its varices being situated every 240° (i.e., ⅔ whorl) around the shell as in most Cymatiidae, rather than aligned up the spire sides as in most other Bursidae; by the operculum having its nucleus two thirds of the way down the abaxial margin, rather than central, adaxial or abapically terminal as in other Bursidae; by its extremely coarsely nodular external sculpture; and by its relatively tall spire, short anterior canal, and very short posterior canal.

Almost all writers of the nineteenth century molluscan iconographies (Kiener, 1842; Reeve, 1844a, fig. 30; Kobelt, 1871; 1878, pl. 9) regarded the forms here treated as species of *Tutufa* as a single variable species (usually placed in *Triton* or *Ranella)*, and used for it the name *Ranella* (or *Triton*) *lampas* (Linnaeus, 1758). Not until E. A. Smith (1914) named some of the supposed varieties were more than a few names applied to the group, and thus the nomenclature is relatively simple compared with that of many Linnaean molluscs, especially Cymatiidae.

Collections and literature I have examined for this study, and especially the anatomy of the species, make it clear that the forms referred to the species *Triton lampas* (or *Bursa rubeta,* etc.) belong in six (or perhaps seven) species of *Tutufa,* three of which are placed in a new subgenus.

In the "subgenus" *Tritonoranella* Oyama, 1964 (here placed as a synonym of *Bufonariella* Thiele, a subgenus of *Bursa* Röding, 1798) two species have been placed in *Tutufa* by some workers, and both consist of three geographic subspecies. In *Tutufa* the six species are the four forms whose nomenclature was debated during the early twentieth century by E. A. Smith (1914), Vanatta (1914) and Hedley (1916a), together with the almost forgotten northern Indian Ocean *Lampas bardeyi* Jousseaume (1894, p. 100) and the recently recognised *T. oyamai* Habe (1973, p. 140, text-fig. 2). As was pointed out by Powell (1967, p. 189), the fundamental point in the nomenclature of *Tutufa* is the identification of the figures cited in synonymy by early authors, for example under *Murex rana* var. *bubo* and var. *rubeta* of Linnaeus (1758, p. 748) and *Tritonium tuberosum* and *T. bufo* of Röding (1798, p. 127, 128). Comparison of shells in various growth stages with figures in several editions of the critical works and designations of several lectotypes and a neotype to stabilise the nomenclature in this study showed that most current nomenclature, based on that suggested by Hedley (1916a) is correct (e.g., Oyama and Takemura 1963; Wilson and Gillett 1971). Identity of individual figures is discussed under the relevant taxa.

## ABBREVIATIONS

In systematic sections, locality lists, and figure captions, commonly cited Musuems and Australian states have been abbreviated as follows:—

### Museums

AIM — Auckland Institute and Musuem, Auckland.

AM — Australian Museum, Sydney.
ANSP — Academy of Natural Sciences, Philadelphia.
BMNH — British Museum (Natural History), London.
NM — Natal Museum, Pietermaritzburg.
NMNZ — National Museum of New Zealand, Wellington.
NMV — National Museum of Victoria, Melbourne.
NZGS — New Zealand Geological Survey, Lower Hutt.
USNM — United States National Museum, Washington, D.C.
WAM — Western Australian Museum, Perth.

**States**
NSW — New South Wales.
Qld — Queensland.
WA — Western Australia.

## MATERIALS AND METHODS

### Anatomy

In search of taxonomic criteria that might confirm or deny the species recognised from shell characters, gross anatomcial investigation of the mantle cavity, cephalic cavity, vas deferens, penis and alimentary system was undertaken of the species of *Tutufa* for which preserved animals were obtainable *(T. bubo, T. bufo, T. oyamai, T. rubeta,* and *Bursa (Bufonariella) ranelloides humilis)*. Radulae also were extracted from these species, and examined by both standard optical techniques and scanning electron microscopy. For comparision a brief survey of the anatomical and radular features of other Bursidae was also undertaken, establishing that Bursidae are completely uniform in gross anatomical features.

*Tutufa* material dissected in this study is as follows: *T. bufo:* one small incomplete animal from North-West Cape, Western Australia, presented to N.Z. Geological Survey by F. Turnbull; two large, well-preserved, complete animals from 30 m, off Osbourne Shoals, Bate Bay, Cronulla, New South Wales, coll. N. Coleman (Australian Musuem, C 73465); 2 of 3 specimens trawled alive at BS. 307, between Bell's Flat and Hutchinson Bluff, Raoul I., Kermadec Islands in 110-120 m, by Mr A. J. Black and Dr F. M. Climo on R. V. "Acheron", 4 April 1973 (N.Z. National Museum, MF 22102). *T. bubo:* one large incomplete animal (mantle missing, gut broken off at anterior end of stomach) from Mauritius, 1871 (Museum of Comparative Zoology, Harvard, No. 3694; shell No. 142885); one small specimen in same condition as above,.0-1 m, Port Ternay, N.W. Mahé, Seychelles, stn. Sy. 21, 10 Feb. 1966 (Academy of Natural Sciences, Philadelphia, 311233); one small specimen in same condition as above two, 0.2 m, between Ambatoloaka and Madirokely, S.W. Nossi Bé, N.W. Madagascar, stn. H56a, 18 and 24 Oct. 1960 (Academy of Natural Sciences, Philadelphia, 253384). *Tutufa oyamai:* one moderately large, complete specimen and one young complete specimen, m.v. "Pele" Mariel King Memorial Expedition stn. ANI/1, S.W. of Tg. Ngabordamlu, Trangan, Aru I., Moluccas, lat. 6°58'S, long. 134°5'E, 27-29 m, 20 June 1970 (Western Australian Museum); one small complete specimen from m.v. "Pele" Mariel King Memorial Expedition stn. KR VI/3-10, N. of Du Rowa, N. of Nuku Rowa, Kai I., Moluccas, lat. 5°32'S, long. 132°41'E, 27-37 m, 11 June 1970 (Western Australian Museum). *Tutufa rubeta:* two excellently preserved, complete, large animals, m.v. "Pele" Mariel King Memorial Expedition stn. C.P.II, 1 mile S. of Tg. Tutuhuhus, Piru Bay, Ceram, lat. 3°15'S, long. 128°10'E, in 0.6 m, 1 June 1970 (Western Australian Museum); a jar of many animals in various states of completeness from Batangas Province, Luzon, Philippine Islands, lat. 13°47'N, long. 120°55'E, 2-9 m, J. E.

Norton colln. (Western Australian Museum, WAM1910-69). *Bursa (Bufonariella) ranelloides humilis* n. subsp: two topo-paratypes from H.M.A.S. "Diamantina" Stn. 6, lat. 33°S, long. 114°37'E, N.W. of Bunbury, Western Australia, 212-226 m, 15 March 1972 (Western Australian Museum, WAM305-72).

## Radula

Radulae of the large species of *Tutufa* were initially prepared for examination by scanning electron microscope. After freeing from all visible tissue they were soaked for at least 24 hours in concentrated potassium hydroxide, and then were cleaned for 1-2 hours in an ultrasonic bath. Specimens appeared completely clean and gleaming after this treatment. About half the ribbon was mounted on an individual SEM stub with double-sided adhesive tape, and lightly coated with carbon and gold-palladium. The other half was mounted on microscope slides in "Euparal" or "Caedax" for standard examination by light microscopy. SEM examination proved extremely unsatisfactory, at least after this amount of cleaning, because of partly dissolved animal tissue coating teeth of most specimens. Therefore most observations and illustrations here are based on light microscopy and the standard type of sketch of microscope mounts, supplemented by some of the scanning electron micrographs.

## Taxonomic criteria: summary

The taxonomic significance of various features of some tonnaceans has long been debated. The point debated longest is whether the position of varices or the possession or lack of a posterior siphonal canal in the outer apertural lip is the more significant guide to position in the Cymatiidae (= genus *Triton,* in 19th Century iconographies) or the Bursidae (= genus *Ranella,* in 19th Century iconographies). The present study demonstrates the correctness of the conclusion of most authors during this century; species with a posterior canal all have three accessory salivary glands, and all have interlocking basal projections on their central radular teeth and, regardless of their variceal position, are related to *Bursa,* in the Family Bursidae; whereas species lacking a posterior canal lack also the third accessory salivary gland and the basal projections of the central radular teeth, and are related to *Cymatium, Charonia,* and *Ranella* in the Family Cymatiidae. The position of varices (thickened outer apertural lips, strengthening the shell edge) reflects only how much shell is added during each of the animal's brief periods of shell increment (Laxton 1970) and it is not surprising that variceal position is a less useful criterion than animal features such as the operculum, radula, and stomach. In this study, similarities were found between many species in their gross anatomy, in their stomach shape and the position of its digestive gland ducts, of the operculum (as shown by the postion of its nucleus) that have dissimilar variceal positions. It is concluded that variceal position is not an important taxonomic criterion. In the classification of Bursidae proposed here, both shells with cymatiid-like varices (at each two-thirds of a whorl) and shells with typically bursid varices (at or near each half whorl) are included in the one subgenus, *Bursa (Bufonariella).* In other words, it is concluded that the features of the operculum, radula, and stomach reflect monophyletic histories, whereas variceal position is a plastic feature which, in some taxa, reflects convergence.

It appears from this study that the operculum is one of the most useful features for higher classification in the Tonnacea, demonstrating subfamily relationships in the Tonnidae and Cassidae, and generic relationships in the Ficidae,Bursidae, and some Cymatiidae. At the generic and specific levels, the features of the radula and stomach are the most useful criteria, in conjunction with the traditional assessment of shell characters. In some groups, the shape of the penis (presumably reflecting species recognition characters or the evolution of physical cross-fertilisation barriers) and whether the seminal duct is open or closed are useful specific and subgeneric criteria. Presumably other criteria will be found in the female reproductive system (beyond the writer's ability).

## ANATOMY

Bursidae have been neglected in anatomical studies until recently. D'Asaro (1969) described the eggs, embryogenesis and early organogenesis of *Bursa (Bufonariella) corrugata* (Perry), figuring larval and early post-metamorphosis anatomy. Houbrick and Fretter (1969) greatly increased our knowledge of the anatomy and ecology of several species of cymatiids and bursids including *Bursa (Lampadopsis) cruentata* (Sowerby), *B. (Lampadopsis) rhodostoma* (Sowerby) and *B. (Bufonariella) granularis* (Röding). They figured the external features of the head-foot of *B. cruentata,* the external features of a complete female *B. cruentata,* and a detailed dissection of the proboscis of *B. granularis,* as well as comparable features and a stomach dissection of *Septa (Cymatriton) nicobaricum* (Röding).

### Anatomy of *Tutufa*

The foot is relatively small and highly contracted in all specimens seen (all removed from shells after preservation) and has a large anterior pedal gland opening as a shallow slit (for example, markedly shallower than in *Tonna variegata cerevesina* Hedley) across the whole front edge of the foot. The cephalic protrusion is relatively small and simple and bears two relatively long, moderately narrow tentacles with a small black eye on a papilla on the outer edge of each tentacle. The tentacles are highly contractile. The proboscis sheath opens as a large, contractile slit on a low snout between the two tentacles. The entire dorsal and lateral surfaces of the cream to fawn head-foot of *T. rubeta, T. bubo* and *T. oyamai* are finely and closely maculated with medium to very dark reddish brown. Those of *Bursa ranelloides humilis* are uniform cream to fawn in well-preserved specimens and, whereas those of *T. bufo* were uniform cream to pale reddish brown in most available specimens, this is apparently because of poor preservation of the epithelium.

The two specimens of *T. bufo* listed above, trawled off Raoul I., Kermadec Is., during 1973 (N.Z. National Museum MF 22102), were dissected to see the external colour of fresh specimens. The head-foot is cream to greyish fawn closely dotted with bright to pale orange-red, and with scattered ill-defined rings of white and pale yellow that are largest and best defined on the dorsal surface of the head. The tentacles are uniform bright orange-red up the eyes, then pale orange shading off to cream over the outer narrow part of each tentacle. Each specimen (one ♂, one ♀) had one tentacle (the right in one specimen, the left in the other) almost lacking darker colour, and the outer tentacle bore fine, closely-spaced, black to brown maculations in a weakly defined ring immediately outside the eye of one specimen, and irregularly placed small patches of similar, fine dark maculations outside the eye of the other specimen. Tentacle colour is evidently highly variable, and not regularly bi-ringed as in the smaller species of *Tutufa.* The hypobranchial gland is very prominent because of its bright vermilion colour. The penis is closely maculated with bright orange red, and has thick rounded edges and a deeply open seminal groove. The proboscis is black, and is expanded to marked lateral lips at its tip, the mouth a wide horizontal slit about a quarter of the width of the flattened proboscis tip.

The cephalic tentacles of *T. oyamai, T. rubeta* and *Bursa ranelloides humilis* each bear two dark brown rings of closely spaced maculations on a cream ground on the outer part of the tentacle beyond the eye, but clearly defined rings are absent in *T. bubo* and *T. bufo*. The rings are similar in *Charonia* but absent in other Cymatiidae I have examined, whereas Cassidae of the subfamily Phaliinae bear two longitudinal dark stripes on the portion of the tentacle beyond the eye, and no transverse rings. The disposition of colour bands on the cephalic tentacles may prove to be a useful guide to relationships in tonnaceans.

The mantle cavity was opened by cutting between the left dorsal ctenidium and the right dorsal hypobranchial gland. The cavity is long and narrow. The pale, grey-brown, mono-pectinate ctenidium is large, long and narrow in all species, with leaflets triangular and longest on the mid-dorsal edge (left edge in dissections). The pale brown, bipectinate osphradium is relatively small, about a fifth to a quarter the length of the ctenidium situated on the left side between the ctenidium and the foot, and placed just behind the incurrent siphon. The hypobranchial gland is large, thick and prominent, but less so in *Tutufa* than in *Bursa (Bufonariella)*, and markedly less so in both than in *Ficus*. In *Tutufa* the external surface of the hypobranchial gland exposed in the mantle cavity is composed of a large, irregularly and closely folded area on the dorsal side of the rectum, with a less well differentiated, only slightly thickened, red-brown, closely folded area in front, between the anus and the excurrent siphon. The gland is the same length as the rectum in all species, and thus differs markedly in length between species. In *Bursa (Bufonariella)* the gland is composed of a flat, markedly thickened, sharply edged, pale red-brown area between the rectum and the ctenidium, with its surface only weakly folded, and with the area in front of the anus only weakly differentiated from the rest of the mantle. The rectum and, in the male, the vas deferens lie between the hypobranchial gland and the foot. The rectum is smooth-walled and ends in a simple anal pore on a short, free, tubular section of rectum, and is slightly broader in *Tutufa* than in *Bursa (Bufonariella)*. The anus is situated well anteriorly, half way down the level of the osphradium, in *T. rubeta;* well posteriorly, half way between the osphradium and the back of the mantle cavity, in *T. bufo;* at the same level as the anterior end of the osphradium (which is placed more posteriorly than in the other species) in *T. oyamai;* and half way down the relatively very large, posteriorly placed osphradium, and thus two thirds of the distance from the back of the mantle cavity towards the anterior, in *Bursa (Bufonariella) ranelloides humilis* (mantle missing from all three specimens of *T. bubo*).

In all species the black-surfaced, pleurembolic proboscis is short, broad and pleated into an anterior point when fully retracted, but may be up to three times its contracted length when expanded, and when fully expanded has a transversely flattened, disc-shaped tip with a marginal rim (Fig. 1b, c) as in *Tonna*. In a few observed specimens of *T. rubeta* and *T. bubo* the lateral edges of the proboscis tip were flattened and extended into small lateral lips similar to the relatively larger ones of *Bursa (Bufonariella) granularis* (Lamarck) figured by Houbrick and Fretter (1969, p.424, fig. 4), and probably such lips can be formed at will by all species of *Tutufa*. The base of the proboscis is attached to the body wall by a ring of closely packed, overlapping, approximately parallel, narrow longitudinal muscles in all species, and in the large *T. (Tutufa) bufo* and *T. (Tutufa) bubo* (but not in *Tutufella)* these are aided by a pair of larger longitudinal muscles that extend further into the cephalic cavity than the other proboscis muscles, one on each side of the proboscis. The base of the proboscis is regularly rounded and not folded in all species of *Tutufa*, but bears a single regular, deep, narrow, and apparently permanent dorsal groove in the two dissected specimens of *Bursa (Bufonariella) ranelloides humilis*.

The large, weakly bilobate, fused cephalic ganglia lie across the oesophagus immediately behind the proboscis, and the nerve ring and lateral nerve plexi are prominent in all species. The mid-oesophagus turns slightly to the right and is then straight and simple, running along the right edge of the floor of the cephalic cavity. Its anteriormost third, from shortly behind the nerve ring, is expanded into the large, saccular, smooth, thin walled, internally deeply pleated oesophageal gland. There is some evidence that the shape of the gland and the presence or absence of small folds in the oesophagus at its posterior end might be useful taxonomic criteria, but dissection of a large amount of similarly-expanded and similarly-preserved material would be needed to confirm this.

Behind the nerve ring most of the cephalic cavity is filled by the large, thin-walled, wrinkled, cream-coloured accessory salivary glands. The true salivary glands are relatively small, equidimensional, medium brown bodies; the right one is centro-dorsal immediately behind the cephalic gangila and of similar size to them, partly enveloped by its two attached accessory glands; the left one lies on the left side alongside the right one to well behind it (the position depends on the degree of extension of the proboscis; in all Bursidae dissected with the proboscis well everted the left salivary gland and its attached accessory gland were markedly posterior). The left accessory gland is much the longest and is narrowly triangular, filling the cephalic cavity behind the other salivary glands, and terminating with its pointed tip in the posterior end of the cavity. The right salivary gland has attached one large and one small accessory gland in all Bursidae examined, the left one much the larger, although only half the size of the left accessory gland; the right one is a small triangular body only about twice the size of the true salivary gland and filling the anteriormost right corner of the cephalic cavity behind the proboscis. In all species the salivary ducts lie alongside the anterior oesophagus and open into the buccal cavity shortly behind the mouth, alongside the odontophore.

The posterior oesophagus passes through the body wall at the back of the cephalic cavity, past the renal gland and pericardium, and joins the stomach through a well-marked sphincter at its anterior end. The cardiac arm of the stomach is a long, narrow, cigar-shaped body with finely and longitudinally pleated, muscular walls, about four to five times as long as its greatest width, passing gradually into the pyloric arm in most species examined but in *T. (Tutufa) bufo* constricted markedly immediately in front of its posterior bend by strongly thickened muscles in the wall. The stomach bends sharply around into the pyloric arm, only half to two-thirds the width of the cardiac arm, only slightly shorter than the cardiac arm, tapered gradually throughout its length to merge imperceptibly into the intestine with no recognisable style sac or terminal sphincter, and with muscular walls whose fine, close, longitudinal pleats continue into the intestine. The anterior digestive gland duct lies in the bend at the posterior end of the cardiac arm. The posterior digestive gland duct lies on the left edge of the venter of the pyloric arm a third of its length from its posterior end, and in all species a small, very narrow typhlosole runs along the left edge of the pyloric arm from the anterior digestive gland duct into the posterior digestive gland duct (major typhlosole, t1?) and from the posterior digestive gland duct forward into the intestine (minor typhlosole, t2?). In almost all bursids examined there is no typhlosole in the cardiac arm, but in *T. (Tutufa) bufo* a prominent fold in the floor of the posterior third of the cardiac arm passes obliquely into the anterior digestive gland duct and is assumed to be an anterior typhlosole. Stomachs of *T. bubo* were not available for dissection, but it seems likely that the constricted base of the cardiac arm and the typhlosole in *T. bufo* are features confined to the subgenus *Tutufa* s. str. and differentiating it from *Tutufa (Tutufella)*. In *T. bufo*, also, the cardiac arm has entirely pleated surfaces, whereas in *T. (Tutufella) rubeta*, the cardiac arm has pleats on its lateral and dorsal walls only, and the anterior end, and in *T. (Tutufella) oyamai* the cardiac arm is entirely smoothly lined (possibly partly because dissected stomaches were distended with unidentified comminuted animal tissue). In all species of *Tutufa* and in *Bursa (Bufonariella) ranelloides humilis* the intestine is straight from stomach to rectum.

In *Bursa (Bufonariella) ranelloides humilis* the stomach (Fig. 10) is smooth and unpleated throughout, apparently lacking typhlosoles also, and has the two digestive gland ducts situated close together near the bend of the stomach, the anterior in the posterior end of the cardiac arm and the posterior in the posterior end of the pyloric arm, separated by a low rounded ridge. A weak differentiation between oesophagus and stomach is probably not a sphincter. Similarly, the stomach of *Bursa (Bufonariella) granulis* (Fig. 1 m) and *Bursa (Bursa) bufonia* (Fig. 1a) lack anterior sphincters and both digestive gland ducts lie near the bend of the stomach, but both species have a small, narrow typhlosole running back down the pyloric arm from the anterior digestive gland duct. *Bursa (Bufonariella) granularis* is unique among the bursids examined in having a well-marked S-shape bend in the intestine, similar to the larger bend of *Tonna*.

In the large *Tutufa bufo* and *T. bubo* the vas deferens is open as a seminal groove for its entire length, and deeply and obviously open along the penis, whereas in the smaller *T. rubeta, T. oyamai* and *Bursa ranelloides humilis* the vas deferens is closed for its entire length, and its course along the penis is visible only as a smooth, faintly raised zone. In *T. bufo* the penis is long and narrow, tapers slightly from base to tip, and has thick, rounded, anterior and posterior edges. In *T. rubeta* the penis has a narrow base and broadens sharply just above the base, then tapers slightly to the tip, and whereas the anterior edge is thick and rounded the posterior edge is thin. In *T. oyamai* the penis has a thin posterior edge as in *T. rubeta* but broadens slightly over the inner two thirds of its length, tapering again slightly over the outermost third. In *T. bubo* the penis is parallel-sided, with a rounded tip and a weakly narrowed base, and with a thin posterior edge as in *T. rubeta* and *T. oyamai*. The penis of *Bursa (Bufonariella) ranelloides humilis* contrasts strongly with those of species of *Tutufa* in having a narrow base and broadening gradually along its length to a broadly rounded, paddle-shaped tip with both anterior and posterior edges thin. In all Bursidae the vas deferens ends at a small, narrowly pointed papilla.

The existence of an open seminal groove in the large species *T. bubo* and *T. bufo*, and presumably also in the closely related *T. bardeyi*, seems to be a fundamental difference from the closed vas deferens of *T. rubeta* and *T. oyamai*, and as it is associated with a minor difference in size and consistent differences in colouration of the cephalic tentacles and in the extent of plication of the columella, it seems best to segregate the species with the two types of vas deferens in two subgenera of *Tutufa*.

The penis of mature *Bursa (Bursa) bufonia* (Gmelin) is flattened and parallel-sided, relatively long and very narrow, only about four times as wide as the closed vas deferens (WAM.835-71, Flying Fish Cove, Christmas Island). A juvenile specimen from Luzon, Philippines with a small, tapered penis and open seminal groove was discussed under the generic diagnosis. Of 14 badly dehydrated specimens of *Bursa* species with black aperture from Batangas Province, Luzon, Philippines (J. E. Norton Colln., Western Australian Musuem, WAM.497-69) the one male has a closed vas deferens. Two specimens of *Bursa (Lampadopsis) rhodostoma* (Sowerby) (Batangas Province, Luzon, Philippines, WAM.495-69; Bataan Prov., Luzon, WAM.1909-69) were both female. *Bursa (Bufonariella) granularis* (Lamarck) has an extremely long, narrow, parallel-sided penis with rounded edges, little more than twice the width of the closed vas deferens (W. of Pt. Cloates, N. Western Australia, on reef, Sept. 1968, W.A.M. Nigaloo Expedition, WAM. 841-71; 11 specimens, 2 small ♂, 9 small to large ♀ ). The three male specimens seen of *Bufonaria margaritula* (Deshayes) have a long, narrow, cylindrical penis only about twice the width of the open seminal groove (9 miles at 125° from Bongao Light, Tawi Tawi Bay, Sulu Archipelago, 1 small ♂, WAM. 839-71; Tayabus Bay, W. Quezon Province, Luzon, Philippines, J. E. Norton colln., WAM. 678-70, large suite; of 8 removed from shell, 6 ♀ and 2 ♂). A single male of *Bufonaria nobilis* (Reeve) from m.v. "Pele" Mariel King Memorial Expedition stn. AH1/5, near Tg. Bt. Kapal, Haruku Is., E. of Ambon I., Indonesia, 82-88 m (WAM. 616-74) has a long, narrow flattened, parallel-sided penis about three times the width of the central, swollen, closed vas deferens. The existence of both an open seminal groove and a closed vas deferens in different species of *Bufonaria* requires further investigation.

The numbers of male and female specimens seen during this study suggest that populations of Bursidae have a sex ratio markedly dominated by females (more than 3 ♀ : 1 ♂ in large suites).

Radula

The radula of *Bursa (Bursa) bufonia* (Gmelin) (Fig. 2a) has a relatively small, low central tooth with a shallowly embayed base, wide basal limbs, small, sharply triangular, basal interlocking processes, and a large, long, narrow, sharply pointed main cusp with one to four small, hooked denticles on each side of its base, the number of denticles varying greatly from one tooth to the next and between the two sides of each tooth. The lateral teeth are large and heavily built, with a long, narrowly pointed cusp bent relatively gently down from the base, with a large, square, high base, and with one to three minute denticles on the outer edge of the cusp and none on the inner edge. The marginal teeth are smooth and gently curved, and the inner has a relatively massive, square base whereas the outer has a small base.

The radula of *Bursa (Bufonariella) ranelloides humilis* (Figs. 2b, 4j, 5a) is similar to that of *B. (Bursa) bufonia* in that the base of the central tooth is shallowly embayed and the interlocking processes are relatively small and triangular. It differs from that of *B. (Bursa) bufonia* in having a smaller and narrower cusp, narrower dorsal portion of the base, and larger denticles on the central tooth, a markedly more strongly hooked lateral tooth with a smaller, narrower base, more numerous denticles on the outer edge and a single small denticle on the inner edge, and (as in all other bursids examined) a lighter base of the inner marginal tooth.

Radulae of all species of *Tutufa* differ from those of *B. (Bursa) bufonia* and *B. (Bufonariella) ranelloides humilis* in having the base of the central tooth markedly more deeply embayed, so that the basal limbs are relatively long, widely spaced, and narrow, and in having longer and narrower interlocking basal processes. The lateral teeth are still more strongly hooked than in *B. (Bufonariella)* and have similarly small bases, and differ from those of all other bursids examined, or figured by other workers, in having highly varied, but usually numerous denticles on both inner and outer edges, those on the inner edge being visible only through the tooth in normal orientation, and not merely a small inner denticle protruding towards the mid-line of the radula as in *B. (Bufonariella)* and most other bursids. Lateral teeth are similar to those of *B. (Bufonariella)*. Individual specific features are discussed below.

## Subgenus **Tutufa** sensu stricto

### **Tutufa (Tutufa) bardeyi** (Jousseaume, 1894).

Figs 9a, b, d; 10a, d

*Lampas bardeyi* Jousseaume, 1894:100 (reprint p.3), "Golfe d'Aden".

*Bursa (Tutufa) rubeta* var. *gigantea.* — E. A. Smith, 1914:230, pl. 4, Fig. 5 (shells from Muscat only).

*Bursa (Bufonaria) rubeta* var. *bardeyi.*— Bayer, 1932:231.

Shell extremely large, up to 360 mm long, i.e. reaching a larger size than any other species of *Tutufa.* Spire relatively tall, of straight outline, tapering regularly to a narrow apex (tip eroded in all specimens seen). External sculpture of low, broad, extremely ill-defined spiral cords, about eight between periphery and neck on last whorl; interstices filled by one or two low, relatively narrow spiral cords; strongly concave shoulder bears three or four low, ill-defined, relatively narrow spiral cords. Spiral cord at periphery raised into sparse, large, anterioposteriorly compressed, well-rounded nodules, with interspaces wider than the nodules; nodules increase in size over each intervariceal space, so that they are largest immediately before each varix. Major spiral cord below periphery raised into lower, sparser, more gently-rounded nodules than those on peripheral row. Shell surface otherwise smooth and lightly polished to weakly malleated in unencrusted individuals. Outer lip varix weak, the slightly flared thin lip edges forming main part of varix of most specimens seen; outer lip extremely flared and varices on spire flared in one old individual. Interior of outer lip uncallused and wrinkled in conformity with exterior spiral cords in most specimens; bearing a narrow noduled ridge in juveniles; thickened but only weakly noduled in the one old individual seen. Inner lip moderately broadly flared, with a thin columellar shield projecting to the left, well-callused in parietal region to form a projecting pad at posterior end of aperture, constricting the prominent, relatively long, widely open anal canal. Parietal region bearing a thin, raised, callous ridge in most specimens, thickened to a nodule in one old individual; below parietal ridge bearing relatively few, sparse, weakly anastomosing, narrow plicae in juveniles, plicae gradually becoming weaker as shells grow so that large specimens bear a few weak denticles low on inner lip, and the one old individual has a thickened inner-lip shield and only a small irregularly wrinkled area on the lower part of the lip. Aperture white. External colour of unencrusted specimens light to medium reddish-brown, maculated with dark reddish-brown between nodules and in corresponding positions on uppermost three or four major spiral cords, the whole crossed by ill-defined wavy, fawn axial streaks. Animal not seen; operculum dark brown, thick, elongate-oval, with nucleus at between half and one-third the height and situated near the abaxial margin.

DIMENSIONS: Height 348 mm, diameter 221 mm, height aperture + canals 227 mm (BMNH 1899.12.27.8, the specimen figured as "*Bursa (Tutufa) rubeta* var. *gigantea*" by E. A. Smith, 1914, pl. 4, Fig. 5); height 270 mm, diameter 168 mm, height aperture + canals 153 mm (WAM, from East Aden Protectorate); up to 360 mm in height (E. A. Smith, 1914, p.230), up to 380 mm (type) or even 400 mm (Jousseaume, 1894, pp.98, 100).

TYPES: Jousseaume (1894, p.98) stated that the 400 mm x 250 mm specimen of *Tutufa bardeyi* "figure déjà dans les galeries du Muséum", and it is assumed that this and the holotype (p.100) are in the Muséum National d'Histoire Naturelle, Paris.

REMARKS: *Tutufa bardeyi* is the form included under *Bursa (Tutufa) rubeta* var. *gigantea* by E. A. Smith (1914, p.230; pl. 4, Fig. 5 only) about which he commented "they appear to have less of the tubercular sculpture shown in Reeve's figure (Reeve 1844a, pl. 9, Fig. 30a, of the lectotype of *gigantea* E. A. Smith = neotype of *bubo* Linnaeus). The two huge specimens available to Smith, from Muscat, Gulf of Oman (BMNH 1899.12.27.8, Fig. 9a, d (Smith's figured specimen, examined by the writer) and 1899.12.27.9, Fig. 9b) are eroded and heavily encrusted with foraminifera, bryozoa, polychaete tubes, calcareous algae, and bivalves *(Plicatula, Chama,* byssal plugs of *Anomia)* and bored by lithophagine bivalves, and the very smooth, brightly coloured surface is visible only on smaller specimens and unusually clean individuals (e.g. Fig. 10a, d).

*Tutufa bardeyi* differs from other species of *Tutufa* in its larger size, more straight-sided spire, more weakly sculptured inner lip, less thickened and more weakly noduled interior of the outer lip, and very much weaker external sculpture. The white aperture is found also in *T. oyamai* and *T. tenuigranosa* which, however, have strongly plicate inner lips. The nearly smooth inner lip is perhaps nearest to that of *T. bubo* which, however, is pink and bears sparse plicae over most of its height, and that of *T. bufo*, which has a red ring around the narrowest part of the aperture. The light to dark reddish-brown colour pattern is markedly brighter than those of almost all other species, and resembles that of *Charonia lampas*. Only occasional specimens of *T. rubeta* have a brighter colour.

Jousseaume's (1894, p.100) original description is meagre: "*Lampas Bardeyi*. Testa gigantea (R. Lampas Lam. simillima), costae spirales laevigatae; labrum intus laevigatum, extus expansum, nec varicosum. Alt. 380; diam. maj. 250; min. 180 millim. Hab. *Golfe d'Aden*", and also (p.98) "*Lampas Bardeyi*, coquille gigantesque qui peut atteindre 40 centimetres de long sur 25 de large; un tres bel exemplaire donné par moi figure déjà dans les galeries du Muséum". The description of the very large size, smooth spiral ribs, and smooth interior of the aperture, together with the comparison with "*Ranella lampas*" (the name Jousseaume consistently used for *Tutufa bubo* of this paper) leave no doubt of the identity of the present species with Jousseaume's name.

DISTRIBUTION: This apparently rare and almost forgotten species occurs in the north-western Indian Ocean, and probably the Red Sea, from Kenya to at least the Gulf of Oman. Throughout its range it is sympatric with *T. bubo*. Most specimens in collections have been supplied by Dr Don Bosch, American Mission in Muscat, and his generosity to malacologists of the world is acknowledged.

LOCALITIES: "Golfe d'Aden", type (Jousseaume, 1894, p.100); Bir Ali and Mukalla, East Aden Protectorate, coll. R. W. George, April 1963 (WAM); Muscat, Gulf of Oman, old individual with thickened, flared aperture, BMNH 1899.12.27.9; Muscat, Gulf of Oman, specimen figured by E. A. Smith (1914, pl.4, Fig. 5), BMNH 1899.12.27.8; Melindi, Kenya, collected alive 1970 (juvenile), BMNH; "Jeffrey's Bay, eastern Cape Province, South Africa", coll. Mrs A. C. Davies, 1964 (almost certainly collected near Mogadiscio, Somalia, where Mrs Davies lived for two years), juvenile, NZGS, WM.10548; Muscat, Oman, NZGS, WM.11582, coll. & pres. D. T. Bosch; Muscat, Oman, USNM 657394, coll. & pres. D. T. Bosch; Muscat Oman, coll. & pres. D. T. Bosch, growth series in American Museum of Natural History.

### **Tutufa (Tutufa) bufo** (Röding, 1798)

Figs 1d, g, p; 2c; 5b, c, f; 6; 11a, c-f; 12a, g

*Tritonium bufo* Röding, 1798:128 (refers to Martini, 1780, 4, pl.129, Fig. 1238).

*Triton lampas*.— Lamarck, 1822:180; Kiener, 1842, *Triton:* pl.5, Fig. 1; Reeve 1844a, *Triton:* pl.10, Fig. 30b (only); Lischke, 1869:47; Lischke, 1871:34; Lischke 1874:29; Kobelt 1871:175, pl.37, Figs 3, 4; Kobelt 1878: pl.9, Fig. 2 (not of Linnaeus, 1758).

*Bursa (Lampas) hians*.—Angas, 1877:179 (Macleay R., N.S.W.) (not of Schumacher, 1817).

*Ranella lampas*.— Tryon, 1881: pl.19, Fig. 12.

*Tritonium lampas* var.— Dunker, 1882:31.

*Tutufa (Crossata) californica*.— Suter, 1906:328 (not *Ranella californica* Hinds, 1843).

*Argobuccinum siphonatum*.— Iredale, 1910:73 (not *Ranella siphonata* Reeve, 1844).

*Bursa (Tutufa) rubeta* var. *lissostoma* E. A. Smith, 1914:230, pl.4, Fig. 3.

*Bursa bubo*.— Vanatta, 1914:80 (in part).

*Bursa siphonata*.— Oliver, 1914:528 (not *Ranella siphonata* Reeve, 1844).

*Bursa bufo*.— Hedley, 1916a:42; 1918:67.

*Bursa (Tutufa) bufo*.— Kira, 1955:43, pl.21, Fig. 20; Kira 1961:55, pl.21, Fig. 20; Kira 1962:57, pl.22, Fig. 20.

*Tutufa lissostoma*.— Iredale, 1931:214, pl.23, Fig. 5; Okutani, 1970:124, pl.8, Fig. 1; Kuroda, Habe & Oyama 1971:134, pl.34.

*Tutufa bufo*.— Iredale & McMichael, 1962:55; Oyama & Takemura 1963: *Tutufa* pl.2, Figs 2-4; Powell, 1967:189, pl.36, Fig. 8 (New Zealand); Wilson & Gillett, 1971:80, pl. 50, Fig. 1.

*Bursa bubo* forma *lissostoma*.— Cernohorsky, 1972:118, pl.32, Fig. 7a.

*Bursa bubo lissostoma*.— Powell, 1974:205.

Shell to ca. 180 mm high, i.e., the smallest species in the subgenus, with short spire, large oval aperture, almost completely smooth inner lip, and pale flesh pink to white aperture bearing a dark brownish to bright red ring around the most narrowly constricted area, immediately inside the flared inner and outer lips. External sculpture of three major rows of anteroposteriorly compressed nodules, those of the uppermost row the largest, narrowly rounded, and protruding as particularly large nodules on varices; remainder of surface sculptured with closely spaced rows of variable, low and obscure to coarse and prominent rugae. Outer lip strongly flared, its outer edge digitated by exterior ribs, bearing eleven or twelve low, narrowly rounded nodules at innermost edge of flare. Inner lip widely flared, with parietal callous pad constricting large, protruding anal siphon and with about three to six low plicae at base of columella, otherwise smooth. Anterior siphonal canal short, curved strongly to the right, so fasciole is large, prominent, and coarsely rugose. Exterior pale reddish fawn to brown, mottled in varied patterns of small, irregular, medium red-brown splashes.

DIMENSIONS: Height 106.5 mm, diameter 65.5 mm (lectotype of *Bursa (Tutufa) rubeta* var. *lissostoma* E. A. Smith); height 135.0 mm, diameter 78.4 mm (WM 10744, Wedge I., WA, NZGS); height 129.8 mm, diameter 84.7 mm (WM 10743, crayfish pot off Rottnest I., WA, NZGS).

TYPES: The holotype of *Tritonium bufo* Röding, 1798, is the specimen figured by Martini (1780, vol. 4, pl.129, Fig. 1238). Its whereabouts are not known to me.

The specimen of *Tutufa (Tutufa) bufo* (Röding) figured by Smith (1914, pl.4, Fig. 3) as *Bursa rubeta* var. *lissostoma* Smith, lodged in the British Museum (Natural History), reg. no. 197384, and figured in colour by Reeve (1844a, pl.10, Fig. 30b) is here designated the lectotype of *Bursa rubeta* var. *lissostoma* E. A. Smith, 1914. The locality was designated by Kuroda, Habe & Oyama (1971, p.134) as Madagascar.

VARIATION: *Tutufa bufo* is quite variable in external sculpture, and some particularly short specimens have coarsely rugose and nodular external sculpture, with a mottled medium and light brown colour pattern. In collections examined almost all such shells came from New Caledonia or Mocambique, but a single short, very coarsely sculptured specimen from Townsville, Queensland, in the Australian Museum (C. 66562) is not distinguishable from New Caledonian shells. Many intermediates exist in the collections examined, and the coarsely sculptured shells are assumed to be part of the normal genetic variation of *T. bufo*.

REMARKS: *Tutufa bufo* differs from *T. bardeyi* in its markedly smaller size, its heavier build, its larger and more elongate aperture associated with a relatively broader last whorl and relatively shorter and broader spire, its prominent row of large, sharp nodules around the shoulder, its markedly coarser external spiral and axial sculpture, its pale fawn to pale marbled reddish-brown colour pattern, and, most notably, by its pale flesh pink to white aperture with a deep red to bright red ring around the most narrowly constricted area of the aperture and with broadly flared lips, the inner completely smooth and the outer bearing one row of low modules. The red ring in the aperture is the most distinctive feature and is found only in this species. It differs from *T. bubo* in its smaller size, its larger aperture, its shorter spire, its smoother inner lip, and in bearing the red ring in the aperture; many specimens of *T. bubo* and *T. bufo* are similar in external colour and sculpture, and juvenile specimens of the two species are difficult to distinguish. It differs from *T. rubeta* in its larger size, its markedly smoother exterior, its shorter spire, its paler colour, in the inner lip being smooth rather than coarsely plicate, and in the interior of the outer lip bearing one row of nodules of the same colour as the lip rather than two prominent rows of pale nodules on a deep red background.

NOMENCLATURE: This is the form named *Bursa (Tutufa) rubeta* var. *lissostoma* by E. A. Smith (1914). Vanatta (1914) first suggested that it is a distinct species from *T. rubeta*, and used the name *bubo* Linnaeus for it. Hedley (1916) questioned Vanatta's identifications of the figures cited by Linnaeus, and introduced the name *bufo* Röding for this species.

Röding (1798, pl.128) cited for *Tritonium bufo* the figure by Martini (1780, vol. 4, pl.129, Fig. 1238). The large figure clearly shows the flaring lip, smoother inner lip, large fasciole, and relatively broad last whorl of the species called *B. rubeta* var. *lissostoma* by E. A. Smith (1914), and the newly coloured copy of this figure given by Kuester & Kobelt (1871, pl.37, Fig. 3) clearly shows the relatively smooth outer surface, the large shoulder nodules, and the red ring around the most constricted portion of the aperture that characterise this species.

The similar names *bubo* and *bufo* have long troubled taxonomists. Linnaeus (1758, p.748; 1767, p.1216) spelled the name *bubo* in both binominal editions of "Systema Naturae", and the spelling is evidently not in error. Dr H. A. Rehder (in litt.) pointed out the words' different etymologies, *bubo* signifying the European horned owl and *bufo* a toad, so that the names are different words. Smith (1914, p.227) and Dodge (1957, p.104) noted that Röding "wrote *bufo* instead of *bubo*, a change suggested by Chemnitz as being a typographical error in the Systema". They evidently considered that Röding (1798) intended *T. bufo* to be the same species as *T. bubo* (Linnaeus), and Smith (1914) regarded them as so. Recently Kuroda, Habe & Oyama (1971, p.135) returned to this point of view, although they applied the name *bubo* to the large, coarsely noduled, pink-mouthed shell here called *T. bubo*, and used *T. lissostoma* (E. A. Smith, 1914) for the species here called *T. bufo*. Their action cannot be upheld as there can be no doubt that the figure cited by Röding (1798) is of the species with the red-ringed aperture. In at least two recent works (Oyama & Takemura 1963; Wilson & Gillett 1971, p.80) the names *bufo* and *bubo* have been used for different species, and so it is proposed to follow the suggestion by Rehder (1974) and stabilise the name *Tutufa bubo* (Linnaeus) for the species named *Bursa rubeta* var. *gigantea* by E. A. Smith (1914), leaving *T. bufo* (Röding) as the name for the species named *Bursa rubeta* var. *lissostoma* by E. A. Smith (1914).

ECOLOGY: Around Australia, New Guinea and New Zealand, specimens of *Tutufa bufo* have not been collected in shallow water, or at all on the offshore islands of the Great Barrier Reef. Specimens have been taken quite commonly alive at times in depths of about 20 to 80 m by scuba divers collecting on rock reefs, such as the suite collected at Osbourne Shoals, Cronulla, Sydney by Mr N. Coleman, and specimens collected at the Poor Knights Islands in New Zealand. Live specimens have also been taken in small numbers consistently over many years by fish and prawn trawlers in depths of about 80 to 150 m from the continental shelf of eastern and western Australia, from about Sydney to Moreton Bay and Fremantle to Houtman's Abrolhos Islands, and lately in northern New Zealand as far south as the Bay of Islands, i.e., wherever extensive fish and prawn trawling has been carried out around northern Australia and northern New Zealand, and thus probably occur throughout the Indo-West Pacific in this habitat.

EGG MASS: Along with several live animals of *T. bufo* from rocks in about 30 m off Osbourne Shoals, Cronulla, Mr N. Coleman collected an egg-mass, now in the Australian Museum (C. 73465). The mass consists of 48 large, simple, elongate capsules, closely packed together but without regular arrangement, on a simple basal membrane. Each capsule is parallel-sided, approximately 23 mm long and 4 mm wide, flattened laterally, with a few low, irregular, ill-defined folds in the walls, and its outer end is hemispherical. All are about 60-70% filled with relatively large, oval eggs, clearly visible to the naked eye, and consisting almost entirely of bright yellow yolk cells. Eggs measured with a micrometer eyepiece were 0.3-0.4 mm in greatest diameter.

In arrangement and simplicity of the capsules, the egg mass of *T. bufo* resembles those of *Argobuccinum pustulosum tumidum* (Dunker) and *Fusitriton magellanicus laudandus* Finlay. However, capsules of *Argobuccinum* and *Fusitriton* are shorter than those of *Tutufa bufo,* and have flat tops with right-angled edges (see also Laxton, 1969, p.250, pl.2). Egg capsules of two other species of Bursidae have been described. That of *Bursa (Bufonariella) corrugata* (Perry) figured by D'Asaro (1969, p.352, Fig. 1A) and those of two specimens of *Bursa (Bufonariella) granularis* (Perry) observed by me in the Western Australian Museum are quite unlike that of *Tutufa bufo* and closely resemble the highly organised, hemispherical masses formed by such Cymatiidae as *Cabestana spengleri* (Perry) and *Septa parthenopea* (von Salis) (see Laxton, 1969, p.250, pl.1). They contain stalked capsules of triangular section arranged in concentric rows inside a hemispherical basal membrane resembling the skin of half an orange. Cernohorsky (1967, p.313, Fig. 2) figured the egg-mass of *Bursa (Bufonariella) granularis* as a very different structure. Relatively short, simple capsules are sparsely set on end in a translucent, oval, gelatinous mass with vertical edges and a concave top; this was probably the egg-mass of a less highly evolved mesogastropod on which the specimen of *C. granularis* was feeding. As *Charonia* has the same poorly organised type of egg-mass as *Tutufa* (Laxton, 1969, p.250) and as that of *Distorsio* is still more simplified than any described here (D'Asaro, 1969, p.369, Fig. 11), tonnacean egg-masses will probably prove to be useful taxonomic criteria when more are described.

RADULA: The radula of *Tutufa (Tutufa) bufo* (Figs. 2c, 5b, c, f) has a relatively low, broad central tooth with relatively broad basal limbs, and has from three to six hooked denticles on each side of the base of the main cusp, the number varying greatly from tooth to tooth and from side to side of one tooth. The lateral tooth has a strongly hooked cusp with numerous but highly varied, hooked denticles on both inner and outer edges.

DISTRIBUTION: *Tutufa bufo* is relatively common on the continental shelf of Western Australia as far south as Cape Naturaliste (Wilson and Gillett, 1971, p.80) and on the continental shelf of eastern Australia to a little south of Sydney, on both coasts as far north as trawling is carried out. Presumably the lack of specimens from northern Australia merely reflects a lack of sampling. It occurs at Lord Howe I., and has been recorded on several occasions as a beach shell at Raoul I. in the Kermadec Islands (Suter, 1906, p.328; Iredale, 1910, p. 73; Oliver, 1914 p.528). Three living specimens were trawled recently off Raoul I. in 110-120 m by Dr F. M. Climo, N.Z. National Museum, from A. Black's R.V. "Acheron". Recently the species has been collected sparsely in northern New Zealand (first recorded by Powell, 1967, p.189). Elsewhere it is recorded from "south of central Honshu, at 10-20 fathoms (18-36 m) depth" (Kira, 1962, p.68) and "Honshu (Boso Peninsula as northern limit), Shikoku and Kyushu . . . On rocks and gravels from 10 m to 50 m deep" and from Sagami Bay (Kuroda, Habe & Oyama, 1971, p.134) in Japan; "Indian Ocean, Madagascar, Red Sea" (E. A. Smith, 1914, p.230); Bouganville, Solomon Islands (Powell, 1967, p.189); Nagasaki, Japan, and Manila (Lischke, 1869, p.47, referring to Reeve, 1844a, fig. 30b); Seychelles Bank, Indian Ocean (Okutani, 1970, p.124, pl. 8, fig. 1); and Dar es Salaam (Spry, 1968, p.18). Lischke (1869, p.47; 1871, p.34; 1874, p.29) and many other early workers recorded *"Triton lampas"* from a large range of localities, but it has usually not been possible to determine which species of *Tutufa* was referred to in each record. No specimens of *T. bufo* were taken by the M.V. "Pele" Mariel King Memorial Expedition to the Moluccas, or by the earlier M.V. "Pele" expedition to the Sulu Archipelago, or in J. E. Norton's extensive collecting in the Philippines (all material from these three examined in the Western Australian Musuem) but this probably merely reflects lack of trawling on the continental shelf. A single specimen has recently been recorded from Hawaii (Fair 1973).

The southernmost specimens seen from the western Indian Ocean are both the short-spired, coarsely sculptured form: low spring tide mark, among rocks in reef, west shore Quissirua Jamal, North-East Islands, Conducia Bay, Moçambique, leg. K. Grosch (NM, H117), the sole specimen seen with weak plicae over whole height of columella; 1 m below low spring tide mark, north of Chacos, southwest Conducia Bay, Mocambique, leg. K. Grosch (NM, H118).

LOCALITIES: **Australia**: 4 alive, 27 m off Osbourne Shoals, Bate Bay, Cronulla, NSW, 22 March 1970, N. Coleman (C 73465, AM); "Triton" dredgings, Sydney Harbour, NSW, Capt. Comtesse, 3 shells recorded by Iredale (1931, pl.23, fig. 5) (C 57794, AM); 24 m, off Shark Pt., Clovelly, NSW, 1966, N. Coleman (C 72751, AM); off Ballina, NSW, AM Swain Reefs Exped., 1962 (C 106123, AM); fish trap off Port Macquarie, NSW, pres. T. A. Garrard (C 106119, AM); fish trap off Trial Bay, NSW, April 1960, pres. J. Kerslake (C 106121, AM); same data., WAM; 9 m, on rocky reef top, off Palm Beach, Gold Coast, southern Qld, coll. J. Laxton (C 106523, AM); trawled in 55 m, off Wide Bay, Qld, T.A. Garrard Colln. (C 66570, AM); trawled off Tin Can Bay, Qld, pres. J. Kerslake (WAM); 130-180 m, north of Cape Moreton, Qld, T. A. Garrard Colln. (C. 64631, AM); off Moreton Bay, Old, 79 m 27°27′22″S, 153°39′E, H.M.A.S. "Kimbla", 29 March 1969 (C 77065, AM); trawled off Southport, Qld, T. A. Garrard Colln. (C 106118, AM); 130-180 m, off Cape Moreton, Qld, A.W.B. Powell Colln. (AWBP 51224, AIM); Townsville, Qld, T.A. Garrard Colln. (short, coarsely sculptured shell — Fig. 11e, f) (C 66562, AM); 60 m, off Beagle I., WA, cray pots, Poole Bros., Dec. 1964 (WAM) Beagle I., WA, cray pots, Poole Bros., April 1962 (WAM); Beagle I., WA, cray pots, Poole Bros., 1964 (N 3958, WAM); 11-18 m, W of Flat I., near Long I., off Onslow, WA, B. R. Wilson on "Davena", 1960, Hawaiian W.A. Exped. (WAM); Onslow, WA, pres. I. Blair (C 90848, AM); 3 km S of Vlaming Head Lighthouse, NW Cape, WA, pres. L. Figgis (C 86156, AM); SE end of Dirk Hartog I., Shark Bay, WA, "Davena", 14 May 1960 (WAM. 949-69); 38 m, Middle channel, Houtman's Abrolhos Islands, WA, J. Seabrook, 1965 (WAM); Houtman's Abrolhos Islands, WA, F.R.V. "Lancelin", March 1963 (WAM); 65 m, off Green Head, WA, pres. Mr Baudain (N 751, WAM); cray pots in 130-160 m, Wedge I., WA, pres. J. Yates (WM 10744, NZGS);

CSIRO stn. 3, 28 Jan. 1964, 128-137 m, beam trawl, 30°06'S, 114°32'E, NW of Jurien Bay, WA (WAM); Jurien Bay, WA, pres. Mrs Parkin (WAM); Cray pots, Jurien Bay, WA pres. Mrs Dobbyn (N 3986, WAM); Cray pot, 4-5 m, Blackledge, WA, FRV "Lancelin", July 1963 (N 4099, WAM); Cray pots, Rottnest I., WA, pres. Mr & Mrs W. Back (WM 10743, NZGS); SW of Rottnest I., WA, 145-150 m, M. V. "Bluefin", 17 Sept. 1963 (WAM); HMAS "Daimantina" Stn. 4, W of Mandurah, 33°33'S, 115°4'E, 110 m, 23 Nov. 1970 (WAM); cray pots, 55 m, off Cape Naturaliste Reef, Poole Bros. on M.V. "Bluefin", March 1962 (WAM).

**Lord Howe I.:** Middle Beach, Lord Howe I., recorded by Hedley (1916, p.41) (C 29189, AM).

**Kermadec Islands:** Empty shells on beach, Denham Bay, Raoul I., T. F. Cheeseman, 1887 (AM 19183, AIM); Denham Bay, Raoul I., W. R. B. Oliver Colln. (MF 11381, NZNM); Raoul I., 75-85 m, "Galathea" Exped., 3 March 1952 (Powell 1967, p.189); BS 307, 3 live in 110-120 m, between Bell's Flat and Hutchinson Bluff, Raoul I., 4/4/1973, F. M. Climo & A. J. Black, R. V. "Acheron" (MF 22102, NZNM); BS 313, 1 empty, 150-200 m, NW of Raoul I., R.V. "Acheron", 4/5/1973 (MF 22122, NZNM).

**New Zealand:** Scuba dived in 30-45 m, Poor Knights Islands, off eastern Northland Peninsula, recorded by Powell (1967, p.189) and specimens in several private collections; in crayfish pots off coast north of Bay of Islands, in colln. Mr G. Clifford, Russell; Doubtless Bay, Northland, live specimens trawled in 90-110 m, in colln. Mrs E. Atkinson, Mangonui; several trawled in shallow water off Rangaungu Bay, Northland, in colln. Mr H. Seelye, Houhora; alive on *Zostera* flat opposite Paua, Parengarenga Harbour, Northland, with *Conus kermadecensis* (Powell 1974, p.205).

### **Tutufa (Tutufa) bubo** (Linnaeus, 1758)

Figs. 2d, 4a, 11b, 12f, 13, 14a, c-d.

*Murex lampas* Linnaeus, 1758:748 (in part, figure by Gualtieri, 1742, pl. 50, fig.D, only; Rondelet, 1555, p.81 (= *Charonia lampas)* was designated lectotype by Beu 1970, p.211); Hanley 1855:286 (in part).

*Murex rana* var. *bubo* Linnaeus, 1758:748.

*Murex lampas* var. *bubo.*— Linnaeus, 1767: 1216; Gmelin 1791:3532.

*Triton lampas.* — Lamarck, 1822:180 (in part); Reeve 1844a, *Triton:* pl.9, fig.30a (only); Lischke 1869:47 (in part); Lischke 1871:34; Lischke 1874:29.

*Bursa lampas.* — Schepman 1909:118.

*Bursa (Tutufa) rubeta* var. *gigantea* E. A. Smith, 1914:230, pl.4, fig. 4 (only).

*Bursa bubo.* — Vanatta, 1914:80 (in part); Hedley 1916a:42; Hedley 1922:165 (use as a trumpet); Cernohorsky 1967a:311, pl.42, fig.1; Cernohorsky 1967b:42, pl.1, fig.1; Cernohorsky 1972:118, pl.32, fig. 7 (only); Salvat & Rives 1975:307, fig. 178.

*Bursa rubeta gigantea.* — McMichael, 1960:78, fig. 159; Rippingale and McMichael 1961:69, pl.7, fig. 20.

*Tutufa bubo.* Oyama & Takemura, 1963: *Tutufa* pl.2, fig. 5; Habe & Kosuge 1966:46, pl.16, fig. 10.

*Bursa lampas* or *rubeta* var. *gigantea.* — Spry, 1968:18, fig. 121.

Shell reaching approximately 300 mm in height, i.e. the second-largest species in the genus, with moderately tall spire, strongly flared apertural lips, uniformly flesh pink to white subcircular aperture, and moderately long anterior siphonal canal with large fasciole. External sculpture of three or more major rows of large, anteroposteriorly compressed nodules, on most specimens largest at periphery and particularly prominent on varices, last whorl of many specimens rendered biangulate by lower row of nodules being almost as large as peripheral ones; remainder of surface sculptured with many closely spaced rows of irregular, narrowly rounded rugae, rendering entire surface coarsely and irregularly nodulose. Outer lip widely flared, its outer edge digitated by external ribs, interior smooth on large adults but bearing a row of 12-14 small, sharp nodules on immature specimens. Inner lip widely flared, with a narrow parietal rib constricting the relatively short anal canal, plicated well inside aperture by low, widely spaced, simple plaits over entire height below parietal rib (Fig. 4a). Fasciole very prominent in a few specimens (Fig. 14a, d) but usually smaller than that of *T. bufo*. Exterior cream to pale brown, finely and irregularly maculated with medium to dark red-brown splashes.

DIMENSIONS: Height 254 mm, diameter 160 mm (neotype of *Murex rana* var. *bubo*); height 222 mm, diameter 125 mm (paralectotype of *Bursa rubeta* var. *gigantea*); height 195 mm, diameter 120 mm (off Southport, Qld, AM, C 69752); height 218 mm, diameter 141 mm (Fiji, NZNM, MF 18474).

TYPES: The neotype (designated below) of *Murex rana* var. *bubo* Linnaeus, also designated the lectotype of *Bursa rubeta* var. *gigantea* E. A. Smith, is in the British Museum (Natural History), No. 1974147; paralectotype of *B. rubeta* var. *gigantea* E. A. Smith also in BMNH, No. 1914.6.29.1.

Neotype and lectotype designations: Hedley (1916) was the first to suggest that the figure cited for *Murex rana* var. *bubo* by Linnaeus (Rumphius 1705, pl.28, fig.C) refers to the species named *gigantea* by E. A. Smith. Rumphius' pl.28, fig. C (available to me in later editions only) is a poorly drawn dorsal view, reproduced in reverse so that the shell appears sinistral, and could refer to almost any species of *Tutufa* (Fig. 12f). Rumphius (1742, p.60) gave the following description of this shell (free translation): *"Buccina tuberosa,* or knobbly kinkhorn. This species is smaller than the preceding *(Buccina Tritonis),* usually only a hand long, wrinkled over the entire body and completely set with knobs, without lustre or elegance, of a dirty white colour, but rare to find, and therefore valuable. The interior is a beautiful white like porcelain, and here it is called Hector". This suggests that Rumphius was describing either the species here called *T. bubo,* or *T. oyamai* Habe. The two figures available to me (Rumphius 1711, pl.28, Fig. C; 1742, pl.28. Fig. C) differ markedly, the surface sculpture being shown more carefully as a markedly finer nodulation in the earlier edition. It is concluded that this figure cannot be certainly identified with a particular species, but probably refers to the species here called *T. bubo* as it is relatively common in shallow water in the Indo-West Pacific and has a pale, flesh-pink aperture that fades to white in many beach shells.

According to Dance (1966, p.53), "no authentic Rumphius shells are now known", and it can safely be assumed that the holotype of *Murex rana* var. *bubo* Linnaeus is lost. Dance (1967) listed species of Mollusca *not* represented in Linnaeus' collection, and although *Murex rana* is not listed, varieties were not considered for the list, and Mr S. P. Dance reports (*in litt.,* August 23, 1972) that there are no specimens of either varieties *bubo* or *rubeta* of *Murex rana* in Linnaeus' collection. Hanley (1855, p.284-5) also makes no mention of Linnaeus having specimens of the varieties of *M. rana,* and Rehder (1974) noted that the specimen identified as *Murex lampas* in the collection of Queen Ulrica of Sweden, worked on by Linnaeus (1764), is a specimen of *Ranularia lotoria* (Linnaeus, 1758). It is concluded that there are no shells in existence that could be considered original type material of *Murex rana* vars. *bubo* and *rubeta* of Linnaeus, 1758, and as the cited figure is not identifiable, a neotype is here designated of *Murex rana* var. *bubo* Linnaeus.

The holotype of *Murex rana* var. *bubo* Linnaeus, the specimen figured by Rumphius (1705, pl.28, Fig. c), presumably came from the island of Ambon, in Indonesia. As is noted above, the shells included in *Bursa rubeta* var. *gigantea* by E. A. Smith (1914, p.230) include two large specimens of *Tutufa (Tutufa) bardeyi* (Jousseaume), and the specimen figured as *Triton lampas* by Reeve (1844a, pl.9, Fig. 30a), which is also the large Philippine Islands shell from the Cuming collection, figured by Smith (1914, pl.4, Fig. 4) and refigured here (Fig. 13b, c). Smith discussed atypical features of the specimens of *T. bardeyi,* and therefore considered the specimen with coarsely nodular external sculpture and pale, flesh-pink aperture as typical of his "variety" *gigantea.* The specimen figured by Smith (1914, pl.4, Fig. 4) and in colour by Reeve (1844a, pl.9, Fig. 30a), lodged in the British Museum (Natural History), and bearing the register number 1974147, is here designated the lectotype of *Bursa rubeta* var. *gigantea* E. A. Smith, 1914. The locality is "Philippine Islands (found on the reefs)" (Reeve, 1844a, pl.9). As was suggested by Rehder (1974, p.12) the lectotype of *Bursa rubeta* var. *gigantea* E. A. Smith, 1914, is here designated the neotype of *Murex rana* var. *bubo* Linnaeus, 1758. The specimen was described by Smith (1914, p.230) and is figured here (Fig. 13b, c). Therefore the name *Murex rana* var. *bubo* applies to the large, coarsely nodulose shell with a pale, flesh-pink aperture, usually regarded as typical *"Bursa lampas"* and named *Bursa rubeta* var. *gigantea* by Smith (1914), leaving the name *Tritonium bufo* Röding, 1798, as the earliest name for the smaller species with a bright red ring in the aperture.

REMARKS: *Tutufa bubo* differs from *T. rubeta* and *T. bufo* in reaching a much greater size (up to about 300 mm), in its uniform pale pink aperture, in its taller spire than that of *T. bufo* and shorter spire than that of *T. rubeta,* in its inner lip bearing more sculpture than that of *T. bufo* but less than that of *T. rubeta,* in its extremely coarsely nodulose external sculpture, and in its colour pattern being paler than that of *T. rubeta,* although similar to that of *T. bufo.* From *T. bardeyi* it differs in its slightly smaller maximum size, its much coarser external sculpture lacking the polish of *T. bardeyi,* its markedly paler colour pattern, its slightly shorter spire and, principally, by the apertural features. The aperture of *T. bubo* is entirely uniform pale flesh-pink (fading to white in dead shells) with one row of low nodules inside the outer lip, lower than those of *T. bufo,* higher than those of *T. bardeyi,* and very different from the two prominent rows in *T. rubeta;* the inner lip is sparsely but prominently plicate on the parietal area and on the interiormost portion of the columella, whereas in *T. bardeyi* the white aperture has only a few faint plications on the columella, the red-ringed aperture of *T. bufo* has a smooth inner lip, and the uniform red aperture of *T. rubeta* has a strongly and closely plicate inner lip.

RADULA: The radula of *Tutufa (Tutufa) bubo* (Fig. 2d) is similar to that of *T. bufo.* The central tooth differs from that of *T. bufo* in its slightly taller form, slightly more deeply embayed base and narrower basal limbs, and in the highly irregular denticles being formed as serrations (often merely weak notches) in a thin flange alongside each edge of the main cusp. The lateral tooth is less sharply hooked than in *T. bufo* and has fewer, smaller denticles on the outer edge, and on the inner edge the denticles are formed as highly irregular serrations on a wide flange, as on the edges of the central tooth. In many teeth the flange on the inner edge is smooth.

ECOLOGY AND DISTRIBUTION: *Tutufa bubo* seems mainly to have been collected on coral reefs, usually below low tide by snorkeling or scuba diving but occasionally intertidally, and a few live specimens have been taken in trawls or dredges from sand substrates on the inner continental shelf of eastern Australia. During the M.V. "Pele"

Mariel King Memorial Expedition to the Moluccas (material examined at Western Australian Museum) only four juvenile specimens of *T. bubo* were obtained, one on an intertidal coral reef and three by dredging in 11-37 m. The only good, large, live-collected specimen from Australia in the Australian Museum was trawled off Southport, Moreton Bay, Queensland (depth not recorded). Occasional live juvenile specimens have been taken close to the northern New South Wales coast as far south as Minnie Water. It is rare in Western Australia. There is one specimen from the Kermadec Islands in the N.Z. National Museum. Elsewhere it is recorded from the Philippine Islands (lectotype; Reeve, 1844a); Dar es Salaam (Spry, 1968, p.18); Zanzibar (BMNH photograph); Rarotonga, Cook Islands (C106115) and Gilbert Islands (C60), both in Australian Museum; Marquesas (Salvat & Rives, 1975, p.307, Fig. 178); Cernohorsky (1967b, p.42) recorded it from "East Africa to Polynesia and the Hawaiian Islands", but I know of no authentic records from as far east as Hawaii; the records by Fair (1973, pl.3) presumably refer to *Bursa latitudo wolfei* n. subsp., not mentioned in her article. The southernmost specimen seen from the western Indian Ocean, apart from the juvenile from off Durban (see under *T. rubeta*), is from 3 m below low spring tide mark, north of Chacos, south-west Conducia Bay, Moçambique, leg. K. Grosch (NM, H119).

LOCALITIES: **Australia:** Trawled off Minnie Waters, N.S.W., November 1, 1963, juvenile (C 70011, AM); beach, Fairfax I., Bunker Group, Qld, J. Booth, 1968 (C 69053, AM); beach, Caloundra, Qld, J. Kerslake Colln. (AM); rubble crest in centre of island, One Tree I., Capricorn Group, Qld, coll. A. G. & J. I. Beu, Dec. 1971 (WM 11581, NZGS); trawled off Southport, Moreton Bay, Qld (C 69752, AM); beach, Cairns, Qld, T. A. Garrard Colln (C 106114, AM); trawled off Cooktown, Qld, Grigg Colln (NMV); 30 m, off Biggada Creek, Barrow I., WA. Aug. 1973 (215 mm high) (WAM).

**Kermadec Islands:** Raoul I., Kermadec Islands, Haylock Colln (MF 8787, NZNM).

### Subgenus **Tutufella,** new name

### **Tutufa (Tutufella) rubeta** (Linnaeus, 1758)

Figs 1b, c, e, j, k; 3; 4g-i; 5d, e; 7; 9c; 12b-e; 14d

*Murex rana* var. *rubeta* Linnaeus, 1758:748 (refers to Rumphius, 1705, pl.28, Fig. D).

*Murex lampas* var. *rubeta.*— Linnaeus, 1767:1216; Gmelin 1791:3532.

*Tritonium tuberosum* Röding, 1798:127 (refers to Martini 1780, vol. 4, pl.128, Fig. 1236-7).

*Triton lampas.*— Lamarck, 1816: pl.420, Figs 3a, b, *Liste,* p.5 (not of Linnaeus, 1758); Lamarck 1822:180 (in part).

*Triton lampas* var.— Kobelt, 1871:175, pl.40, Figs 7, 8.

*Lampas hians* Schumacher, 1817:252 (same Fig. as for *T. tuberosum* Röding).

*Murex lampas.*— Wood, 1828: pl.25, *Murex,* Fig. 28d (not of Linnaeus, 1758).

*Tritonium lampas.*— Anton, 1839:83.

*Lampas caledonensis* Jousseaume, 1881:177 (syntype Fig. E. A. Smith 1914, pl.4, Fig. 2).

*Bursa (Tutufa) rubeta,* typical var.— E. A. Smith, 1914:228, pl.4, Figs 1, 2.

*Bursa rubeta.*— Vanatta, 1914:80; Hedley 1916a:41; Cernohorsky 1972:118, pl.1, Fig. 5.

*Bursa (Bufonaria) rubeta.*— Cooke, 1916:9 (radula).

*?Bursa (Ranella) bubo.*— Adam & Leloup, 1938:151.

*Bursa (Bufonaria) bubo rubeta.*—M. Smith, 1948: pl.10, Fig. 11.

*Tutufa rubeta.*— Oyama & Takemura, 1963: *Tutufa* pl.2, Fig. 1; Habe & Kosuge 1966:46, pl. 16, Fig. 8.

Shell small (to about 110 mm high), with tall spire, short anterior siphonal canal, and small, oval, extremely rugose aperture. Anterior canal bent strongly to the right, but fasciole less prominent than in *T. bufo,* as canal is short. External sculpture of three major spiral cords, the peripheral one (and, in many specimens, lower ones) bearing low, rounded, irregular nodules that protrude little on varices; interspaces completely filled by slightly weaker secondary and tertiary spiral cords, the whole bearing small, rounded, irregularly placed gemmae, so that the overall appearance is more evenly nodulose than in other species. Outer lip flared narrowly, its outer edge digitated by external spiral cords, bearing a row of 12-14 short, rounded nodules on the inner edge of the flare, and a second row of low, elongate ridges further inside the aperture, matching outer nodules in position, separated from outer nodules by a narrow smooth zone; deep red, with nodules pale pink to white. Inner lip bright to deep red, bearing a closely and coarsely anastomosing pattern of paler plicae over its entire height, and a short row of small nodules on parietal callous pad, constricting the short anal sinus. Exterior of clean shells deep to bright red, coarsely and irregularly mottled with paler red.

DIMENSIONS: Height 83 mm, diameter 48 mm (Port Moresby, New Guinea, MF 21548, NZNM); height 91 mm, diameter 53 mm (Madang, New Guinea, C 73398, AM); height 101 mm, diameter 59 mm (One Tree I., Capricorn Group, Qld, WM 11632, NZGS).

TYPES: The holotype of *Murex rana* var. *rubeta* Linnaeus, 1758 is the shell figured by Rumphius (1705, pl.28, Fig. D). Its whereabouts are unknown. Similarly, the shell figured by Martini (1780, vol. 4, pl.128, Fig. 1236-7) is the holotype of both *Tritonium tuberosum* Röding, 1798 and *Lampas hians* Schumacher, 1817. Its whereabouts are unknown also. The syntypes of *Lampas caledonensis* Jousseaume, 1881 are presumably in Muséum d'Histoire Naturelle, Paris; one syntype was figured by E. A. Smith (1914, pl.4, Fig. 2). The figures by both Rumphius (see Fig. 12e) and Martini (see Figs 12b, d) both undoubtedly refer to the species universally known as *Tutufa rubeta,* and there are no nomenclatural complications with this species.

ECOLOGY: *Tutufa rubeta* is collected commonly alive on coral reefs in northern New Guinea (specimens in AM) and specimens were taken quite commonly alive from coral reefs below low tide in the Philippines by divers collecting for J. E. Norton (material in WAM). Two specimens were taken alive in 0.6 m of water on coral in Piru Bay, Ceram, during the M.V. "Pele" Mariel King Memorial Expedition (material in WAM). Common empty shells on beaches and reef flats of outer coral atolls of the Capricorn and Bunker groups, southern Great Barrier Reef, show that the species lives commonly a short distance below low tide in this area. Live specimens have *not* been taken by trawling on the continental shelf, but in both eastern and Western Australia occasional specimens with hermit crabs have been taken from crayfish pots or fish traps, south of the area where live specimens have been collected. Therefore *Tutufa rubeta* seems virtually restricted to coral reefs, although a few specimens apparently occur on other substrates in deeper water at the southern end of its range.

RADULA: In the radula of *Tutufa (Tutufella) rubeta* (Figs 3, 4g-i), the central tooth has narrower basal limbs and slightly longer interlocking basal processes than in *T. (Tutufa) bubo* and *T. bufo* and the relatively few (two or three on most teeth) denticles on each side are situated very close to the base of the cusp. The lateral tooth has a more sharply hooked main cusp than in any other of the examined species of *Tutufa,* and the highly varied denticles are larger on the outer edge than in other species and, on most teeth, increase in size regularly towards the cusp. The denticles on the inner edge of the lateral tooth are highly varied also, and most teeth have only one denticle. A lateral tooth is figured (Fig. 3, lower tooth) in different orientation from usual, turned approximately halfway between normal resting orientation and turned fully outwards, showing that in this orientation the denticles on the lateral teeth of *Tutufa* resemble those of other bursids more than they do in normal rest position.

DISTRIBUTION: Around Australia specimens of *Tutufa rubeta* have been collected from north of Fremantle in southern Western Australia to northernmost New South Wales. Elsewhere it is recorded from "Timor, Goram I., Tonga Is., . . . Islands of Ticao and Luzon, Philippines (Cuming), New Caledonia (Jousseaume)" (E. A. Smith, 1914, p.229); common in collections from Madang and the Port Moresby area, New Guinea (Australian Museum) and from the Philippine Islands, the Moluccas and the Sulu Archipelago (Western Australian Museum), and a few specimens have been seen from Diego Garcia and Mauritius (Australian Museum). I have seen no records from the Pacific as far east as Hawaii.

**Australian Localities:** Reef ca. 10 km NE of Coffs Harbour, northern N.S.W., 64 m, in fish trap, with hermit crab, June 19, 1976, coll. J. Ogg & I. Loch (C 103414, AM); Lady Elliot I., Qld, coll. A. E. Wright, May 1962 (C 69194, AM); Fairfax I., Bunker Group, Qld, many on beach, coll. J. Booth, 1968 (C 69053, AM); common with hermit crabs on main reef flat to east of hut, One Tree I., Capricorn Group, Qld, coll. A. G. & J. I. Beu, Dec. 1971 (WM 11632, NZGS); Tryon I., Capricorn Group, coll. J. Kerslake, Sept. 1954 (C 105985, AM); Broadhurst Reef, E of Townsville, Qld, alive subtidal, coll. I. Loch, Oct. 11-12, 1975 (C 104778, AM); Broadhurst Reef, E of Townsville, Qld, alive subtidal, coll. I. Loch, Nov. 9-10, 1974 (C 105987, AM); Wheeler Reef, NE of Townsville, Qld, empty shell subtidal, coll. I. Loch July 15, 1973 (C 105988, AM); Capre Cay, 22°09'S, 152°46'E, Swain Reefs, outermost Great Barrier Reef, AM Exped. Oct. 22, 1962 (C 72661, AM); South I., Lizard I., Qld, 0.5-12 m, alive off E face, coll. W. F. Ponder & I. Loch, Dec. 13, 1975 (C 104436, AM); Lizard I., Qld, coll. P. H. Colman, I. Loch & W. F. Ponder, Nov.-Dec. 1974 (C 99329, AM); New Year I., 50 km ENE Coker I., Northern Territory, 10°54'S, 133°02'E, beach, coll. P. H. Colman, Nov. 5, 1969 (C 71982, AM); beach, Biggada Ck., Barrow I., WA, Aug. 1973 (WAM); alive, intertidal, North-west Cape, WA, in colln. F. Turnbull, Perth; coast at Warra Station, between Carnarvon and Exmouth, WA, 1973, pres. R. Hancey (C 93317, AM); crayfish pot off Houtman's Abrolhos Islands, WA, in colln. Mr and Mrs W. Back, Perth; crayfish pots set in unrecorded localities off Fremantle, WA (? off Rottnest I.), three specimens, in collns. H. Baker, Fremantle, and Mrs G. Hansen, Perth.

### **Tutufa (Tutufella)** cf. **rubeta** (Linnaeus)

Figs. 10b, c.

A single specimen from Moçambique differs strikingly from all other specimens examined of *T. rubeta* (Linnaeus). Firstly, its external coloration is markedly paler than that of *T. rubeta,* being cream with pale red-brown maculations, rather than the brick to deep red of Pacific specimens. Secondly, the interior of the outer apertural lip is markedly paler than in *T. rubeta* (again, cream rather than bright to deep red) so that the denticles are not set off prominently by their background, and the inner lip is markedly darker than in Pacific specimens, so that the white plicae show up prominently on their dark brown background, rather than all of the inner lip being of almost the same pale to bright red as in *T. rubeta.* Thirdly, the prominent and clearly double row of nodules inside the outer lip of *T. rubeta* corresponds to a single row of longer, lower nodules on the Moçambique specimen, as if the two rows of *T. rubeta* were united across the variceal channel but commenced a little deeper into the aperture. In shell shape and sculpture, apertural shape and lip flaring, and variceal shape and position the specimen agrees in all details with normally coloured specimens of *T. rubeta*.

A normally coloured specimen of *T. rubeta* recorded from Natal by Smith (1914, p.229) is of doubtful location (see below), but undoubted Indian Ocean specimens of *T. rubeta* have been examined in the Australian Musuem collection: C 36429, Mauritius; C 52794, Diego Garcia I., Indian Ocean, Hargraves Colln. Both have the typical two rows of nodules inside the outer lip. So the status of the Moçambique specimen must remain in doubt until more material can be examined from a range of Indian Ocean localities, and especially more from Moçambique, but it seems likely that an un-named taxon of *Tutufa (Tutufella)* (whether a species, or a subspecies of *T. rubeta*, is not clear) occurs in the south-western Indian Ocean.

DIMENSIONS: height 77.6 mm, diameter 44.5 mm.

LOCALITY: Moçambique I., Moçambique, collected and donated A. Enes (G 3444, Natal Museum).

E. A. Smith's South African specimens:

Smith (1906, p.41) recorded a specimen as *"Bursa lampas"* from "Durban Bluff", South Africa. A photograph (Fig. 11b) of this specimen kindly sent by the British Museum (National History) shows it to be a juvenile specimen of *Tutufa (Tutufa) bubo* (Linnaeus), and to judge from its very fresh condition it was probably dredged or trawled out to sea off Durban Bluff rather than collected in shallow water. As *T. bubo* is relatively common in the northern western Indian Ocean it seems possible the specimen really came from off Durban. The specimen is registered as No.1906.7.7.6, labelled "Durban Bluff, G. W. Westcott", and is 34.7 mm high and 22.5 mm in diameter.

Smith (1914, p.229) also recorded under *"Bursa (Tutufa) rubeta,* var.1, typical" a shell from "Port Natal (Brit. Mus.)". A photograph (Fig. 12c) of this specimen kindly sent by the British Museum (Natural History) shows it to be typical *T. rubeta* (Linnaeus). The label reads "Port Natal, J. Sanderson. Reg. No. 1861.7.3.29", so that the specimen was registered in 1861. Mr R. N. Kilburn of the Natal Museum (*in litt.*, April 1972) knows of no modern records of any species of *Tutufa* from South Africa, and strongly doubts that Smith's specimen could have come from Natal. The "Natal" specimen is presumably wrongly localised, and the Durban Bluff specimen may be also.

### **Tutufa (Tutufella) oyamai** Habe, 1973

Figs. 1f, i, l, q, 2e, 4b-f, 15d-i.

*Gyrineum (Lampas) ranelloides.* — Melville & Standen, 1899:163 (not *Triton ranelloides* Reeve, 1844) (Torres Strait).

*?Ranella (Lampas) lampas.* — Martin, 1899:148, pl.23, fig. 346, 346a (Miocene of Java) (not of Linnaeus, 1758).

*?Bursa tenuigranosa.* — Vanatta, 1914:80; Hedley 1916a:42 (?not of Smith, 1914).

*Tutufa tenuigranosa.* — Habe, 1961:47, pl.24, fig. 4; Oyama & Takemura 1963: *Tutufa* pl.1, Fig. 6, 7,; Habe 1964: 76, pl.24, fig. 4 (not of E. A. Smith, 1914).

*Tutufa bubo.* — Wilson & Gillett 1971:80, pl.54, fig.2, 2a (in part not *Murex rana* var. *bubo*

Linnaeus, 1758).

*Tutufa oyamai* Habe, 1973:140, text-fig. 2.

Shell small (to about 75 mm high), with moderately short to moderately tall spire, moderately long anterior siphonal canal, moderately prominent fasciole, and small, uniform white aperture with entirely plicate inner lip. External sculpture of three narrow major spiral cords on last whorl, the peripheral one bearing large, anteroposteriorly compressed, narrowly rounded nodules that are particularly large on varices, but lower cords weakly nodulose; interspaces filled by numerous low, fine, closely spaced, secondary and tertiary spiral cords; entire surface finely and closely gemmate. Outer lip flared narrowly, its outer edge digitated by external ribs, its inner edge bearing a row of 12 to 14 low, paired nodules. Inner lip moderately widely flared into a narrow, thin, parietal and columellar shield, smooth around its outer edge, the more interior portion bearing a row of low nodules on the parietal callous pad, constricting the relatively long, narrow, anal sinus, and coarsely and closely plicate for its entire height below parietal callus. Exterior uniform pale fawn to medium red-brown.

DIMENSIONS: Height 63.2 mm, diameter 46.4 mm (holotype); height 72.0 mm, diameter 47.8 mm (paratype, Taiwan: Habe 1973, p.141); height 73.3 mm, diameter 44.5 mm (Karachi: Habe 1973, p.141); height 60.0 mm, diameter 39.7 mm (paratype, Fig. 15e,h, Taiwan, WM 11274, NZGS); height 55.8 mm, diameter 37.5 mm (64 m, off Fraser I., Qld, WM 10758, NZGS).

TYPES: Holotype (NSMT-MO. 42372) and paratype (NSMT-MO. 42373) in National Science Museum, Tokyo (Habe 1973, p.141); paratype in NZGS (WM 11274).

REMARKS: *Tutufa oyamai* differs from the four species described above in its relatively small size, in having a shorter spire than that of *T. rubeta,* in its thin, light build, and in having crisp, finely nodulous external sculpture formed by low, narrow, well-defined axial growth ridges crossing the many low, narrow, well-defined spiral threads. The aperture is uniformly white with a flared inner lip densely covered with low, narrow, closely spaced, weakly anastomosing plicae, lower and less coarsely anastomosing than in *T. rubeta,* and with the lightly flared outer lip bearing a complexly digitate outermost edge and a single row of small, paired, white nodules or ridges inside. The flared inner lip leaves a small false umbilical hollow below the fasciole, not as large as that of *T. tenuigranosa.*

RADULA: The radula of *Tutufa (Tutufella) oyamai* (Figs. 2e, 4b-f) has a central tooth very similar to that of *T. rubeta* but with even narrower and slightly straighter basal limbs and smaller and sharper interlocking basal processes. The denticles are similarly strongly hooked in the two species. The lateral tooth is markedly less strongly hooked, has a smaller base with fewer protruberances, and has smaller denticles on the base of the cusp than in *T. rubeta.* The outer edge of most specimens has three denticles that are strongly hooked, as on the central tooth, and the inner edge has from none to three denticles (one on most teeth) that are small and obscure.

ECOLOGY: *Tutufa oyamai* is a moderately common species throughout the eastern Indian Ocean and western Pacific ocean. Most specimens have been taken by trawling or dredging on sand substrates in water to about 100 m deep. It is taken not uncommonly around Taiwan by prawn trawlers, and not uncommonly off northern New South Wales and southern Queensland by both prawn and fish trawlers. The M.V. "Pele" Mariel King Memorial Expedition to the Moluccas in 1970 took 14 specimens at eight stations ranging from intertidal coral reefs (one specimen) to dredgings in up to 84 m; most specimens and all live specimens were taken in about 30-55 m.

DISTRIBUTION: Around Australia *T. oyamai* has been taken from northern-most New South Wales around to Houtman's Abrolhos Islands in central Western Australia. Elsewhere it has not been regarded as a distinct species, and records are scarce; it is quite common in collections from Taiwan, the Philippines, and the Moluccas. There are no records from Hawaii or from the western Indian Ocean west of Karachi, and it is apparently restricted to the eastern Indian and Western Pacific Oceans. Habe (1973, p.142) recorded *T. oyamai* from "off Tung Chiang, Taiwan (Formosa) at the depth of 20-50 m" (type) and from Honshu (Wakayama Prefecture) southwards in Japan, and Formosa, China, Philippines, and Karachi.

**Australian Localities:** Fish trap, off Woolgoolga, northern NSW, J. Kerslake Colln. (C 106021, AM); off Cape Moreton, Qld, purchased L. Moore, 1976 (C 103871, AM); off Tin Can Bay, Old, coll. T. Neilsen (C 62479, AM); off Tin Can Bay, Qld, J. Kerslake Colln. (WAM); off Wide Bay, Qld, T. A. Garrard Colln., 5 specimens (C 66561, AM); trawled, 64 m off Fraser I., Qld, J. Kerslake Colln. (WM 10758, NZGS); Great Barrier Reef Exped., 1929, dredge stn. 12, 18-28 m, Penguin Channel, Qld (C 82262, AM); Murray I., Torres Straight, Haddon Colln., the specimens recorded as *Gyrineum (Lampas) ranelloides* by Melvill & Standen (1899, p.163), Fig. 15g (Manchester Museum); CSIRO stn. 208, 27°40'S, 113°20'E, NW of Bluff Pt., WA, 130.8 m, beam trawl, 10 Oct. 1963 (WAM); 65 km W of Cape Jaubert, WA, 40 m, coll. R. W. George on "Dorothea", 13 Oct. 1962 (WAM).

### **Tutufa (Tutufella) tenuigranosa** (E. A. Smith, 1914)

Figs. 15a, c

*Bursa (Tutufa) rubeta* var. *tenuigranosa* E. A. Smith, 1914:231, pl.4, Fig. 6.

*?Bursa tenuigranosa.* — Vanatta, 1914:80; Hedley, 1916a:42 (? not of E. A. Smith, 1914).

*Tutufa tenuigranosa.* — Habe, 1973:139, text-fig. 1.

Shell large (to 210 mm high), with tall spire, moderately long anterior siphonal canal, moderately prominent fasciole, deep but narrow false umbilical chink, and moderately large, uniform white aperture with entirely plicate inner lip. External sculpture of three narrow major spiral cords on last whorl, the upper two bearing numerous, low, rounded, closely spaced nodules that protrude only weakly on varices, the interspaces filled by numerous low, narrow, closely spaced, secondary and tertiary spiral lirae, the whole surface finely and closely gemmate with even, smooth, rounded nodules. Outer lip narrowly flared, its outer edge coarsely fluted but less obviously digitated than in *T. oyamai,* its inner edge bearing about 12 to 14 small, widely spaced nodules, less clearly paired than those of *T. oyamai.* Inner lip moderately widely flared into a thin parietal and columellar shield resembling that of *T. oyamai,* with a low parietal nodule that constricts the short, relatively wide anal sinus, closely and coarsely plicate over entire height below parietal callus. Fasciole relatively narrow, leaving a deep, narrow, false umbilical chink behind columellar callus shield. Exterior cream-yellow flecked with dark brown, similar to those of *T. bubo* and *T. bufo.*

DIMENSIONS: Height 185 mm, diameter 91 mm (lectotype); height 210 mm, diameter 113 mm; height 192 mm, diameter 103 mm (2 Hong Kong specimens; Habe 1973, p.140).

TYPES: Habe (1973, p.139) treated E. A. Smith's figured specimen of *Tutufa tenuigranosa* as a holotype, but it does not have this status as Smith (1914, p.231) stated that the largest specimen was 210 mm high (i.e., he had more than one specimen) and did not designate type specimens for any of the varieties proposed in his 1914 paper. The specimen of *Bursa (Tutufa) rubeta* var. *tenuigranosa* E. A. Smith figured by Smith (1914, pl.4, Fig. 6) is here designated the lectotype of *Bursa (Tutufa) rubeta* var. *tenuigranosa* E. A. Smith. It is an unlocalised shell lodged in the British Musuem (Natural History), bearing the register number 1914.6.29.4 (Fig. 15a).

REMARKS: Habe (1973, p.139) pointed out that *Tutufa tenuigranosa* is a different species from the more common and more widespread *T. oyamai*. It differs from *T. oyamai* in its much larger size, its taller spire, its lower varices that are only weakly hollowed and buttressed behind, its lower peripheral nodules, its slightly more coarsely and sparsely plicate inner lip, its less clearly paired nodules inside the outer lip, and its deep false umbilical chink present in no other species of *Tutufa*. Its size, shape, and external colouration are most like those of *T. bubo* and *T. bufo*, from which it differs in its weak sculpture and its coarsely plicate inner lip.

*Tutufa tenuigranosa* resembles *T. oyamai* closely in one of the apparently diagnostic features of *Tutufella*, the closely and entirely plicate inner lip, and so is tentatively referred to *Tutufa (Tutufella)*. Examination of the seminal groove will be necessary to confirm its subgeneric location.

DISTRIBUTION: the lectotype and paralectotypes are unlocalised. Recorded by Habe (1973) from about 200 m, off Hong Kong, in the South China Sea. Recent records by shell collectors are from prawn trawlers off Taiwan, and there are two immature specimens from Taiwan in the National Science Museum, Tokyo (NSMT 48445), with a specimen of *Bursa ranelloides ranelloides*. *T. tenuigranosa* seems to occur only in deep water in the South China Sea.

Fossil record of *Tutufa:*

The only records of fossils that presumably belong in *Tutufa* are from the Neogene and Quaternary of Indonesia. Most references to these faunas list only *Ranella* or *Bursa lampas*, with no figures to show which species was intended: Schepman (1907, p.181), post-Tertiary of the Celebes; Martin (1919, pp.88, 132), general faunal lists; van der Vlerk (1931, p.241), general faunal list. Altena (1942, p.108) identified his material from the Kendeng beds of East Java (Pleistocene) as *"Bursa (Ranella) rubeta* (Roeding)", referred to Smith's (1914) revision, but did not refer to any of Smith's "varieties" or figure his specimens. The sole identifiable figure is that by Martin (1899, p.148, fig. 346, 346a) whose figure of *"Ranella (Lampas) lampas"* appears to be of *Tutufa (Tutufella) oyamai* Habe. The specimen is recorded as "Ein Exemplar aus der Menengteng — Schlucht, in Cheribon", Java (Miocene).

## Genus **Bursa** Roding, 1798

### Subgenus **Bufonariella** Thiele, 1929

For synonymy and type species see p.        above. The two species considered below have been thought to be related to *Tutufa* by some recent authors, and Kuroda, Habe & Oyama (1971, p. 133) went so far as to provide a subfamily Tutufinae to include *Tutufa* and *Bursa (Bufonariella) ranelloides* (Reeve), presumably because the varices of *B. ranelloides* are arranged in the same cymatiid-like manner as are those of *Tutufa*. However, it is shown above that the stomach, opercular, radular and apertural features of *B. ranelloides* are closely similar to those of *Bursa* and especially of its subgenus *Bufonariella*, so variceal position is considered to be an insignificant criterion and *B. ranelloides* is placed in *Bufonariella*. *Bursa ranelloides* and *B. latitudo* have their varices aligned up the spire sides on the earliest few spire whorls, in any case, and come to resemble *Tutufa* species progressively down the shell. The two species discussed below superficially resemble

*Tutufa,* however, and have been considered related to it by some authors, and so are revised here.

DISTRIBUTION: The two *Tutufa*-like species of *Bursa (Bufonariella)* considered in this paper have remarkably wide distributions for species of Bursidae. Fig. 20 shows the distribution of the three subspecies recognised in each species. Beu (1976b) discussed the distribution of *Bursa (Bufonariella) ranelloides,* a member of a group of very few species (all Tonnacea) found in the Atlantic, off South Africa, in Australasia (Western Australia only, in this case) **and** in Japan, apparently dispersed around the Southern Ocean by the circum-polar current during Pleistocene time. Occurring in eastern Australia, Hawaii, and the western Atlantic, *B. latitudo* appears to represent a formerly much wider distribution in the West Pacific, and was presumably dispersed to the Atlantic through Panama before late Pliocene time, when the Panama seaway closed. The two species are sympatric only in the Caribbean Sea at present.

### **Bursa (Bufonariella) latitudo** Garrard, 1961

Shells from eastern Australia, Hawaii and the western Atlantic Ocean, discussed by Wolfe (1975), are here considered to belong in a complex of subspecies closely related to *B. ranelloides* (Reeve). *Bursa latitudo* differs from *B. ranelloides* in reaching a markedly larger adult size, in having a taller spire, in having the sculptural cords and nodules arranged very similarly but markedly narrower, with wider spaces and more numerous interstitial spiral cords between primary spiral cords, and the nodules more pointed than corresponding ones of *B. ranelloides,* in having a more sharply and widely reflected outer lip, in having prominent sculpture on the inner and outer lips, and in having the red-brown parietal colour patch partly to completely masked by the parietal plicae on large specimens.

The animal and operculum of *B. latitudo* are unknown and thus the generic position will remain slightly in doubt until the position of the opercular nucleus is described, but the external sculpture and the plication and colouring of the inner lip are so strongly similar to those of *B. ranelloides* that a position in *Bursa (Bufonariella)* seems highly likely.

### **Bursa (Bufonariella) latitudo latitudo** Garrard, 1961

Figs. 16 g-i

*Bursa latitudo* Garrard, 1961:15, pl.2, fig.2.

Specimens of the *B. latitudo* complex from Queensland are of very similar proportions to those of *B. latitudo wolfei* n.subsp. from Hawaii, but differ from Hawaiian specimens in their consistently smaller and more narrowly pointed major nodules, much finer and more closely spaced interstitial spiral cords and rows of fine nodules, and more sparsely and narrowly plicate inner lip callus that becomes more thickened with age so that the parietal colour patch is not visible on large shells.

DIMENSIONS: height 95 mm, diameter 55 mm, height of aperture less posterior sinus 26 mm (holotype; Garrard, 1961, p.15); height 54.4 mm, diameter 33.5 mm, height of aperture plus canals 26.3 mm (C 66528); height 57.0 mm, diameter 34.4 mm (C. S. Wolfe colln.).

Holotype (F.21,111) in National Museum of Victoria.

DISTRIBUTION: The subspecies has been taken only rarely, off southern

Queensland, in water more than 100 m deep. Only three specimens have been seen during this study. The paratype recorded by Garrard (1961, p.15) is a broken and encrusted specimen of *Ranella australasia* (Perry) (Australian Museum, C 63353).

LOCALITIES: trawled off Moreton I., Southern Queensland, in 230 m, holotype (F21,111, NMV); 100-130 m, off Caloundra, southern Queensland, T.A. Garrard Colln., one specimen (C 66528, AM); trawled in 110 m, ENE Cape Moreton, southern Queensland (collection of Charles S. Wolfe, Fort Worth, Texas).

### **Bursa (Bufonariella) latitudo natalensis** Coelho & Matthews, 1970.

Figs. 16a-f.

*Bursa finlayi.*— McGinty, 1962: 39, pl.3, fig. 1 only (paratype), not conspecific with holotype).

*Bursa (Colubrellina) natalensis* Coelho & Matthews, 1970:1, Fig.1-3.

*Bursa (Colubrellina) tenuisculpta natalensis.* — Abbott, 1974:167.

The western Atlantic subspecies of *Bursa latitudo* is distinguished from *B. latitudo latitudo* by its extremely elongate form, more closely and coarsely plicate inner lip especially on the lower part of the columella, markedly more strongly plicate outer lip with plicae extending further on to the flared section of the outer lip than in either of the other subspecies, and moderately to markedly coarser interstitial sculpture. In addition the peripheral and basal rows of nodules of some specimens are markedly larger and more anteroposteriorly compressed than those of *B. latitudo latitudo,* but this is not a consistent difference as nodule size is much more variable in *B. latitudo natalensis* than in the eastern Australian form.

DIMENSIONS: height ca. 50 mm, diameter ca. 20 mm (holotype of *B. natalensis,* dimensions not stated, calculated from scaled illustration); height 82.5 mm, diameter 39.2 mm (paratype of *B. finlayi);* height 73.6 mm, diameter 33.9 mm (USNM 735915, off Nevis, British West Indies).

TYPES: Holotype of *B. natalensis* in Museu Nacional, Rio de Janeiro (no. 3527) (Coelho & Matthews 1970, p.4); paratype of *B. finlayi* in USNM (673601).

REMARKS: Comparison of the holotype and paratype of *Bursa finlayi* McGinty (McGinty 1962, p. 39), loaned by the U.S. National Museum, showed that they belong in two different species. The holotype (Fig. 19a, b) is a small, strongly noduled specimen of *B. ranelloides tenuisculpta* (Dautzenberg & Fischer) resembling the common form of *B. ranelloides ranelloides* from Japan, and similar coarse variants and intergrading more finely sculptured specimens have been seen from several Caribbean *B. ranelloides tenuisculpta* populations (Figs. 19c-g). The paratype (Figs. 16c,d) is an extremely narrow and elongate, coarsely sculptured specimen agreeing closely in all its details, except its larger peripheral nodules, with the holotype of *B. (''Colubrellina'') natalensis* Coelho & Matthews, 1970 (Coelho & Matthews 1970; illustration copied as Fig.16a). Another Caribbean shell, from off Nevis, British West Indies, has the same interstitial sculpture, extremely tall spire, and coarse apertural plicae as in the holotype of *B. natalensis,* but has markedly weaker peripheral nodules (Fig. 16f) and it is concluded that the holotype of *B. natalensis* is a moderately coarsely sculptured specimen, the Nevis shell is a weakly sculptured specimen, and the paratype of *B. finlayi* is a very coarsely sculptured specimen of the same taxon, here regarded as a geographic subspecies of *B. latitudo* Garrard, and not closely related to *Bursa (Colubrellina) condita* (Gmelin), type species of

*Colubrellina* Fischer. Wolfe (1975, fig. 3) illustrated a small, weakly sculptured specimen of the Caribbean form he called *B. finlayi,* and two specimens in his collection have been examined through the courtesy of Col. Wolfe. The shells are similar to the specimen from Nevis and to the holotype, and confirm the distinctive features of the Atlantic subspecies (Figs. 16b,e). These shells all have similar faint, red-brown, axial colour streaks and a large number of fine, closely spaced interstitial spiral threads that distinguish them readily from specimens of *B. ranelloides tenuisculpta,* even when the coarsely sculptured outer-lip flange is broken off (as in the Nevis specimen).

LOCALITIES: crayfish (= spiny lobster) pots in 40-50 m off Pirangi, near Natal, Rio Grande do Norte, Brazil, holotype and four paratypes of *B. natalensis;* fish trap in 220 m, Bay of Matanzas, Matanzas, Cuba, J. Finlay, March 1961 (paratype of *B. finlayi,* USNM 673601); shell trap in 230 m, WSW of Charlestown, Nevis, British West Indies (USNM 735915); fish trap in 180 m, off Bahia de Anasco, west coast of Puerto Rico, two specimens in colln. Charles S. Wolfe, Fort Worth, Texas.

### **Bursa (Bufonariella) latitudo wolfei** n.subsp.

Fig 17

*Bursa lampas.* — Tinker, 1952:98; 99, centre fig. (not *Murex lampas* linnaeus, 1758).

*Bursa finlayi.* — Wolfe, 1975:12, fig.1,2 (not *B. finlayi* McGinty, 1962).

Shell large for subgenus, relatively thick and heavy, relatively wide as in *B. latitudo latitudo* but with the coarse sculpture of *B. latitudo natalensis.* Varices aligned up spire sides on initial three to four teleoconch whorls, but becoming progressively more widely spaced down shell so that they are situated at each two-thirds of a whorl on the last one or two whorls. Aperture large and oval, with thickened and strongly reflected inner and outer lips, and short, widely open anterior and posterior siphonal canals. Outer lip white, coarsely plicate along inner edge of reflected flange by about 15 short, narrow ridges. Inner lip white except for a large, deep brownish red parietal colour patch, mostly masked by the large, closely spaced plicae on mature shells; plicae similar to those of *B. latitudo natalensis* on lower columellar area, but markedly wider, straighter, less anastomosing, and more closely spaced on parietal area than in *B. latitudo natalensis,* so that two especially wide, slightly convex plicae border the posterior canal. Sculpture of one row of peripheral nodules, on most specimens prominent and strongly anteroposteriorly compressed; one row of smaller nodules around a slight basal angulation; two rows on the shoulder, one between the peripheral and basal angles, about four on the base, and four or five fasciolar rows of small, closely spaced nodules; and numerous finely beaded tertiary and quaternary cords. Exterior pale reddish brown, with diffuse medium reddish brown zones between pale nodules on most spiral cords, on varices, and in faint axial streaks.

DIMENSIONS: height 95.0 mm, diameter 56.4 mm (holotype); height 104.4 mm, diameter 58.3 mm (paratype, Honolulu Aquarium); height 94.4 mm, diameter 51.0 mm (small-noduled paratype, collection S. Handrahan, Honolulu); height 92.7 mm, diameter 53.2 mm; height 73.0 mm, diameter 45.6 mm (two paratypes in collection Charles S. Wolfe, Fort Worth, Texas).

HOLOTYPE (BPBM 8936) presented to Bernice P. Bishop Museum, Honolulu, by Charles S. Wolfe; two paratypes in collection Charles S. Wolfe, Fort Worth; one paratype (the specimen figured by Tinker 1952) in Honolulu Aquarium; one paratype in collection S. Handrahan, Honolulu.

LOCALITIES: crab trap, 58 m, off Makaha, Oahu, Hawaii (holotype); crab trap, 120 m, off Kahuku, Oahu, Hawaii (one paratype, C. S. Wolfe Colln.; one paratype, S. Handrahan Colln.); crab trap, 120 m, off Haleiwa, Oahu, Hawaii (small paratype, C. S. Wolfe Colln.); Nanakuli, Oahu "deep water" (paratype, Honolulu Aquarium). Apparently endemic to Hawaii.

REMARKS: *Bursa latitudo wolfei* differs from *B. latitudo latitudo* in having markedly coarser nodules, especially between the primary spiral cords, and in having markedly coarser and more closely spaced apertural plicae, especially on the inner lip. It is similar in shape to *B. latitudo latitudo* and similar in sculpture to *B. latitudo natalensis*, but differs from *B. latitudo natalensis* in its considerably wider shape, shorter ridges inside the outer lip, and wider and more closely spaced plicae on the inner lip.

The sharing of shape with the eastern Australian *B. latitudo latitudo* and of sculpture with the western Atlantic *B. latitudo natalensis* makes the Hawaiian form a neat geographical and morphological intermediate between the other two widely separated populations, supporting the contention that all three are geographic subspecies of a single species.

The new subspecies is named in honour of Charles S. Wolfe, now of Fort Worth, Texas, who loaned or arranged loans of the only Hawaiian specimens the writer has seen and who has contributed several interesting articles on Hawaiian Bursidae and Cymatiidae to "Hawaiian Shell News".

### **Bursa (Bufonariella) ranelloides** (Reeve, 1844)

*Bursa ranelloides* differs from *B. latitudo* in its smaller size (rarely over 65 mm high), its coarser sculpture of rounded rather than sharply pointed nodules, its more strongly excavated inner lip which retains the bright red-brown parietal colour patch at all sizes, and in having markedly fewer interstitial spiral gemmate cords.

The record of "*Gyrineum (Lampas) ranelloides*" from Murray I., Torres Strait, by Melvill and Standen (1899, p.163) was based on juvenile specimens of *Tutufa (Tutufella) oyamai* Habe, as shown by one of their specimens kindly loaned by Mr C. Pettitt, Manchester Museum (Fig. 15g). Hedley (1909, p.31) also recorded "*Gyrineum ranelloides*" from Queensland, but presumably merely on the basis of Melvill and Standen's record as there are no specimens from eastern Australia in any collections I have examined. Therefore *B. ranelloides* and *B. latitudo* apparently are sympatric in the western Atlantic Ocean only, although they occur sympatrically with other species of *Bufonariella*, especially *B. (Bufonariella) granularis* (Röding), in all areas they inhabit.

*Bursa (Bufonariella) ranelloides* has developed three geographic subspecies, the nominate one in Japan (and, doubtfully, the Philippines), *B. ranelloides tenuisculpta* (Dautzenberg & Fischer) from the eastern and western Atlantic (Azores, type locality) and South Africa, and *B. ranelloides humilis* n. subsp. from central and southern Western Australia.

### **Bursa (Bufonariella) ranelloides ranelloides** (Reeve, 1844)

Figs 18d, f-i

*Triton ranelloides* Reeve, 1844a: pl.3, Fig. 10a, 10b; Reeve, 1844b:118; Lischke 1871:37.

*Simpulum papillosum* A. Adams, 1870:419.

*Ranella cruentata.*— Tryon, 1881:267 (in part not *Bursa cruentata* Sowerby, 1835).

*Bursa ranelloides.*— Kuroda & Habe, 1952:43.

*Buffonariella* [sic] *ranelloides.*— Habe, 1961:47, pl.24, Fig. 3.

*Bufonariella ranelloides.*— Habe, 1964:76, pl.24, Fig. 3; Beu 1971:110, pl.8, Fig. 8 (holotype *Simpulum papillosum* A. Adams); Kuroda, Habe & Oyama 1971:134, pl.33, Figs 5, 6.

*Tritonoranella ranelloides.*— Oyama, 1964:332.

The nominate subspecies reaches about 80 mm high, although it is rarely more than 65 mm high. The sculpture consists of a very weakly developed subsutural row of nodules, an upper peripheral row of five to nine medium to large, widely spaced, well-rounded nodules in each intervariceal space, a lower peripheral row of rounded nodules that are slightly smaller and slightly more closely spaced than in the upper row, a further row of smaller rounded nodules below the periphery in some specimens, and the basal and intermediate peripheral spiral cords bear low and sparse nodules. The spire is moderately tall, and the varices are broadest at the upper peripheral row of nodules. The colour is cream, closely and finely maculated with pale reddish brown, with prominent darker red-brown patches on the varices and between all large nodules. The parietal colour patch is deep reddish-brown to "purple" (Reeve) and the apertural plicae are relatively weakly developed, and fine and close on the inner lip.

DIMENSIONS: Height 49.6 mm. diameter 32.2 mm (holotype of *B. ranelloides*); height 55.8 mm, diameter 33.2 mm (Tosa Bay, Shikoku, WM 11277, NZGS); height 50.0 mm, diameter 29.4 mm (Sagami Bay, Honshu, WM 11276, NZGS); height 56.8 mm, diameter 35.5 mm (Kuroda, Habe & Oyama 1971, p.134, pl.3, Fig. 5); height 79.3 mm, diameter 43.7 mm (Kuroda, Habe & Oyama 1971, p.134, pl.3, Fig. 6; Sagami Bay, Honshu).

TYPES: Reeve (1844a, pl.3, Figs 10a, b) had only one specimen of *Triton ranelloides*, and it is here regarded as the holotype. Photographs of the specimen kindly sent by the British Museum (Natural History) (Figs 18d, f) show that the shell (BMNH 1967594) is a worn, partly polished beach shell 49.65 mm high, with large nodules, closely resembling large-noduled Japanese shells (e.g., Fig. 18i). The worn nodules show the white inner shell material, but between the nodules the shell surface is sculptured exactly as in Japanese shells and bears a very similar colour pattern to that of Japanese shells (*see* also Reeve, 1844a, pl.3, Figs 10a, b — the specimen had a markedly brighter colour pattern in 1844 than it has now). Reeve (1844a, caption to p.3, Figs 10a, b) gave the locality "Matnog, Province of Albay, Island of Luzon, Philippines (found on the reefs); Cuming". The species has not subsequently been recorded from the Philippines, and the holotype so very closely resembles southern Japanese specimens that there can be little doubt that Cuming attached the wrong locality to this shell, among the many other wrong localities that have been recorded in his collection, and that the holotype is a beach shell from southern Japan. Dr Tadashige Habe has lent me a specimen trawled off Cebu, Philippine Islands (NSMT 55501, National Science Museum, Tokyo). It is a small, narrow, medium red-brown specimen with extremely narrow, small, sharply pointed nodules, closely resembling the Japanese small-noduled specimens included in their var. *tenuisculpta* by Dautzenberg & Fischer (1906, pl.2, Figs. 19, 20), but not closely resembling the large-noduled, beach-worn holotype of *Bursa ranelloides*. It occurred with a specimen of *Bursa rehderi* Beu, 1978, recorded from depths of 208-640 m off the Philippines, so probably this sample was taken in deep water and represents the southern limit of the north-west Pacific subspecies. Japanese shells are here considered to constitute the nominate subspecies of *B. ranelloides*, and *Simpulum papillosum* A. Adams (holotype (BMNH 1967680) figured by Beu 1971, pl.8, Fig. 8; type locality "Takano-Sima, Japan") is synonymised with *B. ranelloides.*

DISTRIBUTION: Recorded from five stations in Sagami Bay at 65-87 m depth by Kuroda, Habe & Oyama (1971, p.134); "Boso Peninsula, Honshu, and southwards" (Habe, 1964, p.76); "Honshu (Boso Peninsula as northern limit), Shikoku, Kyushu . . . On sandy bottom of 50-200 m deep" (Kuroda, Habe & Oyama 1971, p.134). Taiwan, dredged with two *Tutufa (Tutufella) tenuigranosa* (E. A. Smith) (NSMT 48445); off Cebu, Philippine Islands (NSMT 55501).

### **Bursa (Bufonariella) ranelloides tenuisculpta** Dautzenberg & Fischer, 1906

Fig. 19

*Bursa ranelloides* var. *tenuisculpta* Dautzenberg & Fischer, 1906:36, pl.2, Figs 15-18.

*Bursa (Tutufa) tenuisculpta*.— Morrison, 1949:10; Abbott 1954:198.

*Bursa finlayi* McGinty, 1962:39, pl.3, Figs 1a, 2, 3 (*not* Fig. 1); Abbott 1974:167.

*Bursa tenuisculpata* [sic]. — Scheltema, 1972:864, Figs 1c, 2a.

*Bursa (Colubrellina) tenuisculpta*.— Abbott, 1974:166, Fig. 1778.

Specimens of *B. ranelloides* from South Africa and the Caribbean and Dautzenberg & Fischer's coloured figures (1906, pl.2, Figs 15-18) of shells from the Azores and Madeira differ from Japanese specimens in their slightly smaller size; their taller and narrower form brought about mainly by a taller spire; in having only a pale reddish-brown or, in large specimens, even completely absent parietal colour patch; in having the varices broadest at the lower peripheral row of nodules or, in specimens where the peripheral nodules are very large, in having the varices about equally broad at both peripheral angles; in having extremely coarse, prominent, widely spaced, strongly anastomosing plicae on the inner lip and equally strong simple ones on the outer lip, the two series both passing well out on to the flared lips; and in having smaller and markedly more sharply pointed external nodules of different arrangement. Atlantic shells have the following sculpture: a subsutural row of fine, low, closely spaced nodules of the same size as those in the lower peripheral row, markedly larger than those in the subsutural row of *B. ranelloides ranelloides;* seven to 13 small, relatively close, sharp nodules in each intervariceal space in the upper peripheral row; smaller and closer nodules than above in the lower peripheral row; and an intermediate peripheral row and several basal rows of small, close nodules very little smaller than those in the lower peripheral row. The colour pattern lacks the large dark patches on the varices and between the nodules of Japanese shells.

Atlantic and South African specimens thus differ consistently from Japanese ones in their colour, shape, apertural plicae, and sculptural details, especially the sharper nodules. The Japanese population is highly variable in sculpture and at least 20% of Japanese shells approach Atlantic ones in the fineness of the nodules (as is to be expected between subspecies), but the nodules remain sharper and the shape remains different in Atlantic specimens. A similar range of variation in nodule size is seen in Atlantic shells; the holotype of *Bursa finlayi* McGinty (discussed under *B. latitudo natalensis*) and similar shells are coarsely noduled specimens of *B. ranelloides tenuisculpta* resembling *B. ranelloides ranelloides* in the size of their peripheral nodules, but in Atlantic populations only about 20% of specimens are as coarsely sculptured as Japanese shells. Atlantic and South African specimens are here considered to belong in a distinct geographic subspecies, for which the name *tenuisculpta* is available.

DIMENSIONS: Not stated by Dautzenberg & Fischer (1906); lectotype approx. 68 mm high, 38 mm wide (from their pl.2, Figs 15, 16, at natural size); height approx. 43 mm, diameter approx. 25 mm (paralectotype, Madeira, Dautzenberg & Fischer 1906, pl.2, Figs 17, 18); height 48 mm, diameter 20.5 mm (holotype of *Bursa finlayi* McGinty); height 63 mm, diameter 35 mm (NM 9928, SE of Durban Bluff, South Africa).

TYPES: Dautzenberg & Fischer (1906) included Japanese finely-sculptured specimens (e.g., their pl.2, Figs 19, 20) in their var. *tenuisculpta*. Therefore the specimen from off the Azores figured by Dautzenberg & Fischer (1906, pl.2, Figs 15, 16) is here designated the lectotype of *Bursa (Lampas) ranelloides* var. *tenuisculpta* Dautzenberg & Fischer, 1906. The lectotype is presumably in the Oceanographic Institute, Monaco. The holotype of *Bursa finlayi* McGinty is in USNM (634570).

DISTRIBUTION: Scheltema (1972, Fig. 4) recorded larval shells of *Bursa (Bufonariella) ranelloides tenuisculpta* from many Atlantic localities in plankton tows, from the eastern Caribbean along the north coast of Brazil, from the coast north of Cape Verde to the Gulf of Guinea, and in a single sample off Angola. With this width of distribution of larvae the occurrence of the subspecies in the eastern Atlantic, in the western Atlantic from the Florida Keys to the West Indies, and in South Africa is not surprising, and the dispersal of occasional specimens seems quite feasible between the widely distributed populations (Atlantic-South Africa, Japan, Western Australia) here considered to be geographic subspecies of the single species *Bursa ranelloides*.

LOCALITIES: **Eastern Atlantic:** "Expedition of 1897: Stn. 899, depth 200 m. Princess Alice Bank, Azores. One living example" (lectotype of *tenuisculpta;* translated from Dautzenberg & Fischer, 1906, p.36); "expedition of 1901: Stn. 1242, depth 240 m. Banc de Seine, Madeira. Six dead examples" (translated from Dautzenberg & Fischer, 1906, p.36). **Western Atlantic:** 215° off Sombrero Key Light, Middle Florida Keys, 210 m, "Triton" Sta. 615, July 8, 1951 (holotype of *Bursa finlayi* McGinty, 1962, USNM 634570); 180-550 m, north of the Virgin Islands (USNM 430336); "Eolis" sta. 146, 180 m, off Key West, Florida (USNM 417778); State Univ. Iowa dredge sta. 29, Bahia Honda, Cuba (USNM 543506); dredged, 230 m, Dry Tortugas, Florida, 1971 (two excellent specimens in collection Charles S. Wolfe, Fort Worth); "The U.S. National Museum collections include specimens dredged in from 50 to 125 or more fathoms [90 to 230 m], from off Sand Key and Key West, Florida; off Bahia Honda, Cuba; from north of the Virgin Islands; and from the Arrowsmith Bank, Yucatan" (Morrison, 1949, p.10), presumably the basis of the record by Abbott (1954, p.198) from "South-east Florida and the West Indies. Dredged on rare occasions". **South Africa:** off Tugela River mouth, Natal, in 37 m, donated G. Scott, November, 1972, two dead specimens (Figs 19h, j) (A12, NM); trawled south-east of Durban Bluff, Natal, in 275 m, donated G. Scott, August, 1972, one dead specimen (Figs 19i, k) (9928, NM).

### **Bursa (Bufonariella) ranelloides humilis** n. subsp.

Figs 1o, r; 2b; 4j; 5a; 18a-c, e.

*Gyrineum ranelloides.*— Verco, 1912:219, pl.16, Figs 6, 7; Hedley, 1916b:196 (not of Reeve, 1844).

Specimens of *Bursa ranelloides* dredged off southern and south-western Western Australia differ from both *B. ranelloides ranelloides* and *B. ranelloides tenuisculpta* in their small size (up to 45 mm high); their relatively very short spires, very short siphonal canals, and very strongly inflated last whorls, producing much shorter and broader shells; in having sculpture of more nearly uniform-sized rows of nodules, the upper peripheral row smaller than in *B. ranelloides ranelloides* and of similar size to that of *B. ranelloides tenuisculpta* and the other rows all relatively coarser than in both the other subspecies; in their uniform pale straw-yellow colour, with only faint reddish-brown patches on the last few varices of large specimens; in their small but bright blood-red parietal colour patches; and in their apertural plicae being less prominent and sparser than in *B. ranelloides tenuisculpta* and more prominent than in *B. ranelloides ranelloides* and not extending as far out of the aperture as in either of the other subspecies. The external sculpture consists of one subsutural row of coarse nodules of the same size as those in the lower peripheral row, an upper peripheral row of 4-10 medium-sized, slightly quadrate, slightly pointed, moderately closely spaced nodules in each intervariceal space, a lower peripheral row of nodules that are only slightly smaller and closer than in the upper peripheral row, and an intermediate peripheral row and several basal rows that are relatively very coarsely noduled, the uppermost two basal rows having nodules only slightly smaller than in the lower peripheral row. The anterior siphonal canal is consistently very short, and very strongly twisted to form a broadly rounded fasciole extending well to the left of the inner lip. The large number of Western Australian shells seen are remarkably consistent in their distinctive features and form a well-defined geographic subspecies.

DIMENSIONS: Height 40.2 mm, diameter 27.8 mm (holotype); height 45.1 mm, diameter 29.3 (figured large paratype, WAM. 310-72); height 43.8 mm, diameter 28.2 mm (dissected topoparatype); height 24.7 mm, diameter 15.9 mm (small figured paratype, WAM. 309-72).

TYPES: Holotype (WAM 305-72) and nine paratypes (WAM 305-72, WAM 309-72, WAM 310-72, WAM 312-72) in Western Australian Museum.

RADULA: The radula and operculum were described and figured by Verco (1912, p.219) and more have been available in this study to confirm Verco's descriptions. The operculum is lanceolate, with the nucleus at the pointed abapical end, and bright yellow-brown. The radula (Figs 2b, 4j, 5a) resembles that of *Bursa* rather than that of *Tutufa* in its central tooth having a shallowly embayed base with relatively small interlocking basal processes. It differs from that of *Bursa (Bursa) bufonia* in having a narrower base to the cusp and larger denticles on the central tooth, and in having markedly smaller and more numerous cusps on the lateral teeth.

LOCALITIES: WAM 305-72, 33°S, 114°37′E, North-west of Bunbury, W.A., 212-226 m, H.M.A.S. "Diamantina", DM. 1/72 stn. 6, live holotype, two live adult paratypes, 1 live juvenile paratype; WAM 309-72, 34°14′S, 114°27′E, West of Cape Hamelin, W.A., 190-161 m, H.M.A.S. "Diamantina" stn. 19, three live paratypes; WAM 310-72, 33°15′S, 114°36′E, north-west of Bunbury, W.A., 161-165 m, H.M.A.S. "Diamantina" stn. 25, one live paratype; WAM 312-72, 32°43′S, 114°48′E, south-west of Mandurah, W.A., 192-179 m, H.M.A.S. "Diamantina" stn. 29, two live paratypes. The following material identified by the writer is also referred here: South Australian Museum, live specimen trawled in 185 m, Great Australian Bight 130 km west of Eucla, by Sir Joseph Verco (Verco, 1912, p.219); N4348, north-west of Rottnest I., W.A., on sponge, 155 m dredged B. R. Wilson on "Bluefin", 15 Aug. 1962 (WAM); N4339, north-west of Rottnest I., W.A., on sponge and sand, 199-214 m, dredged B. R. Wilson on "Bluefin", 14 Aug. 1962 (WAM); south-west of west end of Rottnest I., W.A., 130 m, dredged B. R. Wilson on "Bluefin", Sep. 1965 (WAM).

The following H.M.A.S. "Diamantina" material obtained by Dr B. R. Wilson during 1972 has not been examined personally, but was identified by Dr Wilson (all in Western Australian Museum): WAM 306-72, 33°S, 114°41′E, north-west of Bunbury, W.A., 183 m, stn. 7 (one live); WAM 307-72, 34°S, 114°28′E, west of Cape Freycinet, near Margaret River, southern W.A., 195-219 m, stn. 12 (one live); WAM 308-72, 34°25′S, 114°36′E, west south-west of Cape Leeuwin, southern W.A., 146-142 m, stn. 17 (one live); WAM 311072, 32°45′S, 114°47′E, south-west of Mandurah, W.A., 220 m, stn. 28 (one live); WAM 313-72, 32°S, 115°6.7′E, west of Garden I., W.A., 176-182 m, stn. 33 (one live); WAM 314-72, 33°S, 114°37′E, north-west of Bunbury, W.A., 219-221 m, stn. 6/11 (12 dead); WAM 315-72, 34°S, 114°28′E, west of Cape Freycinet, W.A., 195-219 m, stn. 12 (one dead); WAM 316-72, 34°S, 25.5′E, west south-west of Cape Leeuwin, W.A., 190-174 m, stn. 16 (two dead); WAM 317-72, 34°15′S, 114°30′E, west of Cape Hamelin, W.A., 219-274 m, stn. 18 (one dead); WAM 318-72, 34°14′S, 114°27′E, west of Cape Hamelin, W.A., 190-161 m, stn. 19 (two dead); WAM 319-72, 33°44′S, 114°26.1′E, south-west of Cape Naturaliste, W.A., 238-183 m, stn. 21 (four dead); WAM 310-72, 32°45′S, 114°47′E, south-west of Mandurah, W.A., 220 m, stn. 28 (two dead); WAM 321-72, 30°58′S, 114°49′E, west north-west of Lancelin, W.A., 212-215 m, stn. 41 (2 dead); WAM 322-72, 30°10′S, 114°13′E, west north-west of Jurien Bay, W.A., 178-179 m, stn. 48 (one dead); WAM 323-72, 29°43.5′S, 114°20′E, north-west of Beagle I., W.A., 183 m, stn. 52 (one dead); WAM 324-72, 29°58′S, 114°27′E, north-west of Green Head, W.A., 197-219 m, stn. 64 (one dead); WAM 325-72, 31°16′S, 114°54′E, south-west of Ledge Point, W.A., 274 m, stn. 74 (one dead) (a total of 25 localities).

SUMMARY: classification of the Bursidae that have been assigned to *Tutufa*

Genus *Bursa* Röding, 1798

Subgenus *Bufonariella* Thiele, 1929.

*Bursa (Bufonariella) latitudo latitudo* Garrard, 1961, E. Australia.

*latitudo natalensis* Coelho & Mathews, 1970, W. Atlantic.

*latitudo wolfei* n.subsp., Hawaii.

*ranelloides ranelloides* (Reeve, 1844), Japan.

*ranelloides humilis* n.subsp., W. Australia.

*ranelloides tenuisculpta* Dautzenberg & Fischer, 1906, E. & W. Atlantic & South Africa.

Genus *Tutufa* Jousseaume, 1881

Subgenus *Tutufella*, new name for *Lampas* Schumacher, 1817,

*Tutufa (Tutufella) oyamai* Habe, 1973, West Pacific & E. Indian Ocean.

*bubo* (Linnaeus, 1758), Indo-West Pacific.

*bufo* (Röding, 1798), Indo-West Pacific.

Subgenus *Tutufella*, new name for *Lampas* Schumacher, 1817, *Tutufa (Tutufella) oyamai* Habe, 1973, West Pacific & E. Indian Ocean.

*rubeta* (Linnaeus, 1758), Indo-West Pacific.

*tenuigranosa* (E. A. Smith, 1914), South China Sea.

?n. sp. aff. *rubeta* (L.), Moçambique.

## ACKNOWLEDGEMENTS

I wish to thank Dr B. R. Wilson and his staff, Western Australian Museum, Drs B. J. Smith and T. A. Darragh, National Museum of Victoria, Dr Helene Laws, South Australian Museum, and Dr W. F. Ponder and his staff, Australian Museum, for the loan of much material without which this paper would have been impossible and for much help during my 1971 visits; Dr A. W. B. Powell and Mr W. O. Cernohorsky, Auckland Institute and Museum, Dr F. M. Climo, N.Z. National Museum, Dr T. Habe, National Science Museum, Tokyo, Drs J. D. Taylor and P. B. Mordan and Mrs K. M. Way, British Museum (Natural History), Dr R. N. Kilburn, Natal Museum, Mr C. Pettitt, Manchester Museum, Dr K. Boss and Mr G. D. Buckley, Museum of Comparative Zoology, Harvard University, and Dr R. Robertson, Academy of Natural Sciences, Philadelphia, for the loan of many specimens; Dr Habe, and Mr F. Turnbull, Perth, Mr & Mrs W. Back, Perth, and Mrs J. Kerslake, Sydney, for the gift of specimens; Dr Ponder for helpful discussions on the anatomy and, in particular, for the use of his extensive loose-leaf index of Australian Mollusca, up-dated from one begun by Charles Hedley; Professor Emily H. Vokes, Tulane University, and Dr H. A. Rehder, U.S. National Museum, for helpful discussions on bursid taxonomy; Dr W. K. Emerson, American Museum of Natural History, and Dr J. Rosewater, U.S. National Museum, for information on *Lampas bardeyi* Jousseaume; and Dr Ponder and Mr I. Loch, Australian Museum, Dr R. K. Dell, N.Z. National Museum, and Dr P. A. Maxwell, N.Z. Geological Survey, for comments on the manuscript. Initial research was undertaken at the Australian Museum, Sydney, during 1971 and I wish to thank the Director and staff for hospitality, the Board of Trustees for a grant in aid of research, and the N.Z. Department of Scientific and Industrial Research for fares. Scanning electron micrographs were taken by Mr B. Burt and Mr J. Simes, N.Z. Geological Survey, on a Cambridge Steroscan at Physics and Engineering Laboratory, DSIR; photographs in Figs. 9b, 11b, d, 12c, 13a, 15a, 18d, f are by British Museum (Natural History), in Figs, 15c, i were sent by Dr T. Habe, in Figs 10a, d, 11e, f, 12g, 14b, c, 15b, 16g, i are by A. G. and J. I. Beu, and the rest by messrs D. L. Homer and L. Laronde, N.Z. Geological Survey.

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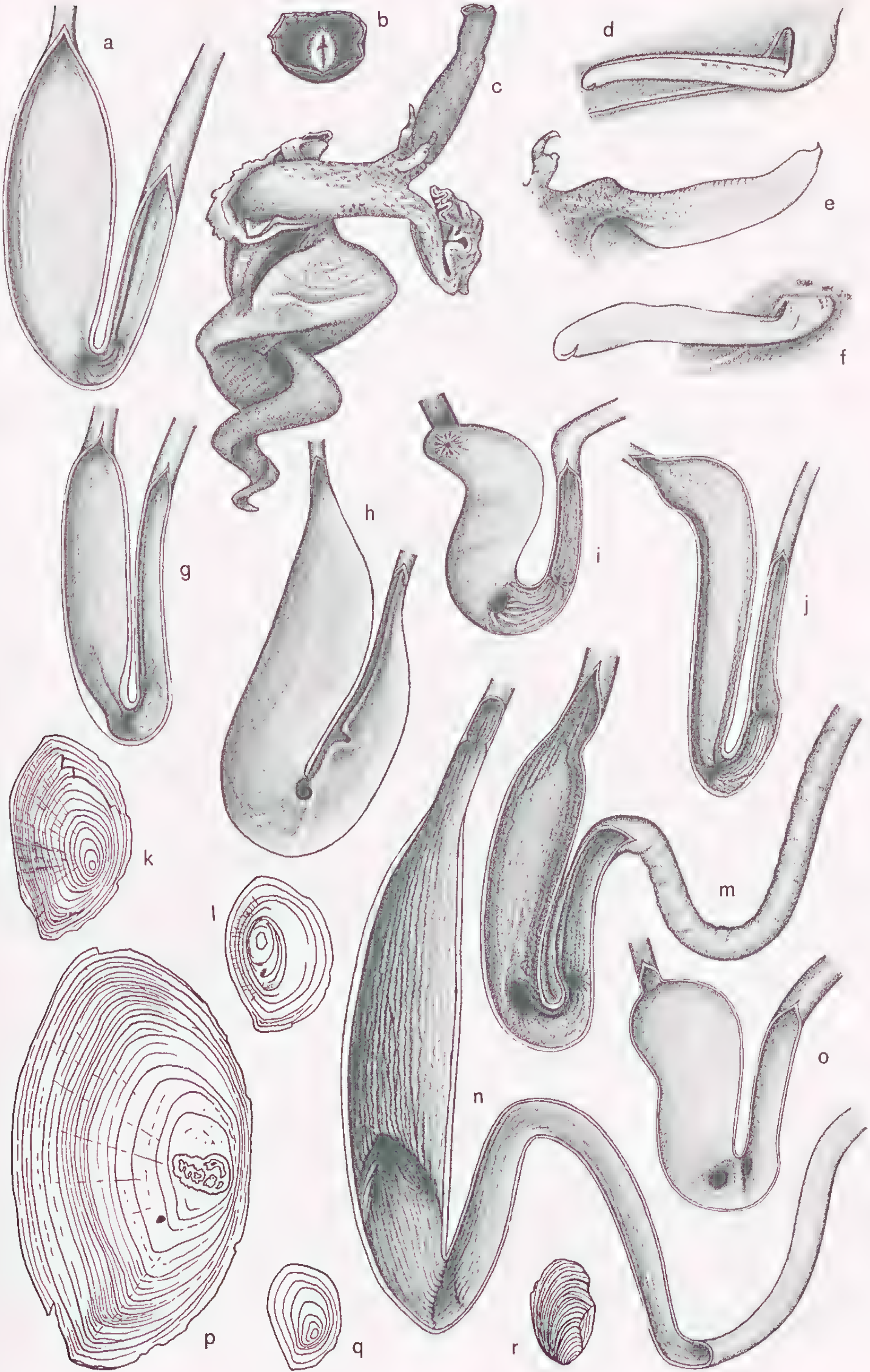
**Fig. 1 a, g-j, n-o** stomachs of tonnaceans, opened by mid-dorsal section (not to scale). **a.** *Bursa (Bursa) bufonia* (Gmelin), Flying Fish Cove, Christmas Island; WAM 835-71. **g.** *Tutufa (Tutufa) bufo* (Röding), off Osbourne Shoals, Bate Bay, Cronulla, N.S.W.; AM, C 73465. **h.** *Charonia lampas rubicunda* (Perry), F. R. V. "Kapala" stn. 71-37-04, east of Broken Bay, N.S.W., 230 m; AM, C 79170. **i.** *Tutufa (Tutufella) oyamai* Habe, m.v. "Pele" Mariel King Memorial Exped. Stn. ANI/1, S.W. of Tg. Ngabordamlu, Trangan, Aru I., Moluccas, 27-29 m; WAM. **j.** *Tutufa (Tutufella) rubeta* (Linnaeus), m.v. "Pele" Mariel King Memorial Exped. stn. CPII, 1 mile S.W. of Tg. Tutuhuhus, Piru Bay, Ceram. 0.6 m; WAM. **m.** *Bursa (Bufonariella) granularis* (Röding), W of Pt. Cloates, N Western Australia, on reef, WAM 841-71. **n.** *Tonna variegata cervesina Hedley,* Bay of Islands, New Zealand; NZGS. **o.** *Bursa (Bufonariella) ranelloides humilis* n. subsp., paratype, H.M.A.S. "Diamantina" stn. 6, N.W. of Bunbury, Western Australia, 212-226 m; WAM 305-72. **b, c.** Complete animal of female *Tutufa (Tutufella) rubeta* (Linnaeus) removed from shell; mantle retracted, proboscis partly expanded (X1). b. — anterior view of proboscis tip (X2), showing lips around central mouth. Same specimen as in Fig. 1j. **d-f.** Penes of *Tutufa* (not to scale). d. — *Tutufa (Tutufa) bufo* (Röding), lateral view, same specimen as Fig. 1g and Fig. 6. **e.** *Tutufa (Tutufella) rubeta* (Linnaeus), dorsal view of penis lying forward; same specimen as Fig. 1b, c, j and Fig. 7. f. — *Tutufa (Tutufella) oyamai* Habe, lateral view, same specimen as Fig. 1i. **k, l, p-r.** Opercula of Bursidae, all enlarged X1.5. **k.** — *Tutufa (Tutufella) rubeta* (Linnaeus), same specimen as Fig. 1b, c, j and Fig. 7. 1, **q.** — *Tutufa (Tutufella) oyamai* Habe, two specimens showing abnormal and normal nuclear position, same locality as Fig 1f, i. **p** — *Tutufa (Tutufa) bufo* (Röding), off Osborne Shoals, Bate Bay, Cronulla, N.S.W.; AM, C 73465. **r** — *Bursa (Bufonariella) ranelloides humilis* n. subsp., paratype, same specimen as Fig. 1o and Fig. 8.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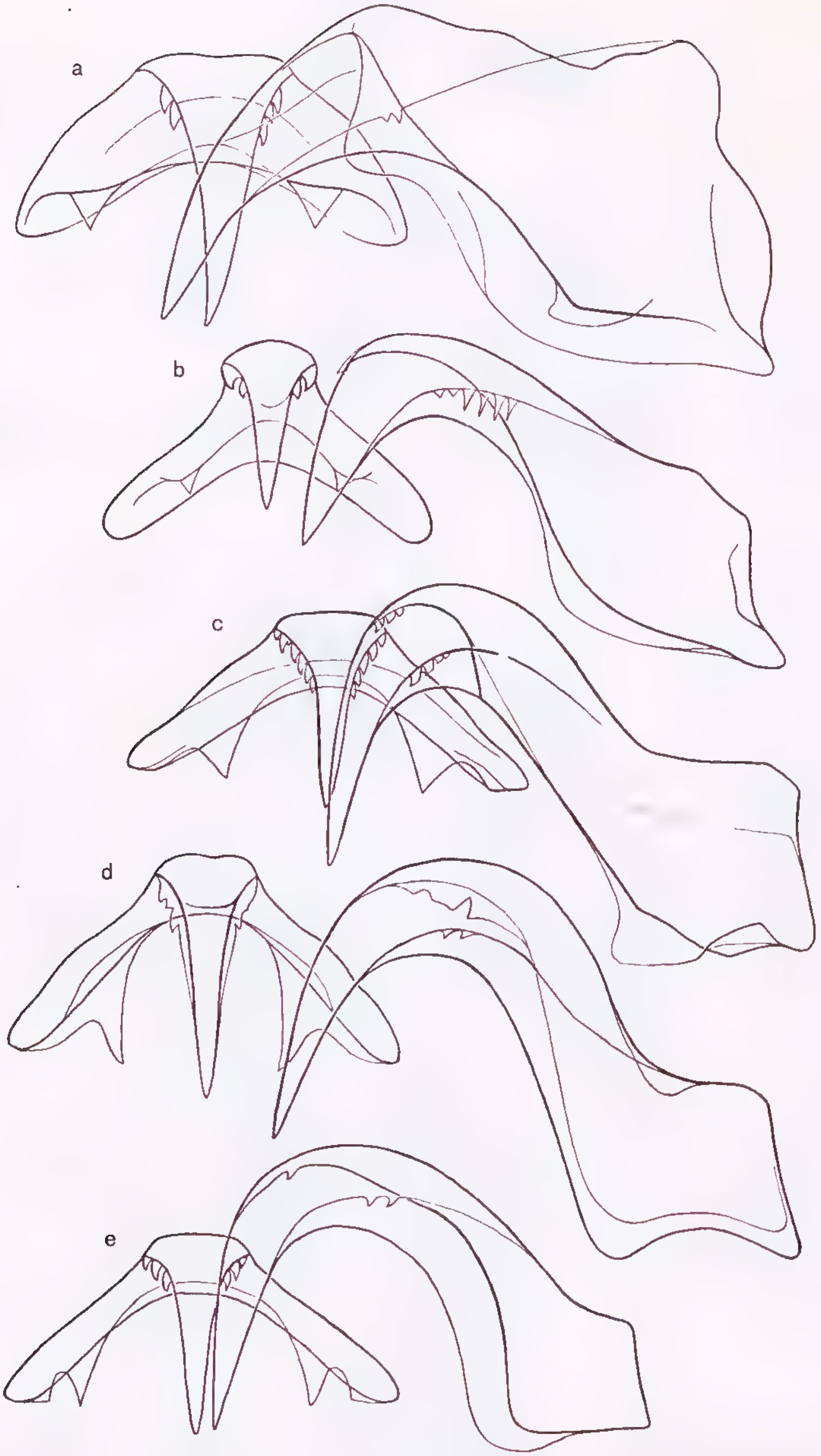

**Fig. 2.** Central and lateral teeth from half of one row of radula of Bursidae (not to scale). **a** *Bursa (Bursa bufonia* (Gmelin), Flying Fish Cove, Christmas Island; WAM 835-71. **b.** *Bursa (Bufonariella) ranelloides humilis* n. subsp., paratype, H.M.A.S. "Diamantina" stn.6, N.W. of Bunbury, Western Australia, 212-216 m; WAM 305-72. **c.** *Tutufa (Tutufa) bufo* (Röding), off Osbourne Shoals, Bate Bay, Cronulla, N.S.W.; AM, C 73465. **d.** *Tutufa (Tutufa) bubo* (Linnaeus), Port Ternay, N.W. Mahé, Seychelles; ANSP 311233. **e.** *Tutufa (Tutufella) oyamai* Habe, m.v. "Pele" Mariel King Memorial Exped. stn. ANI/1, Aru I., Moluccas; WAM.

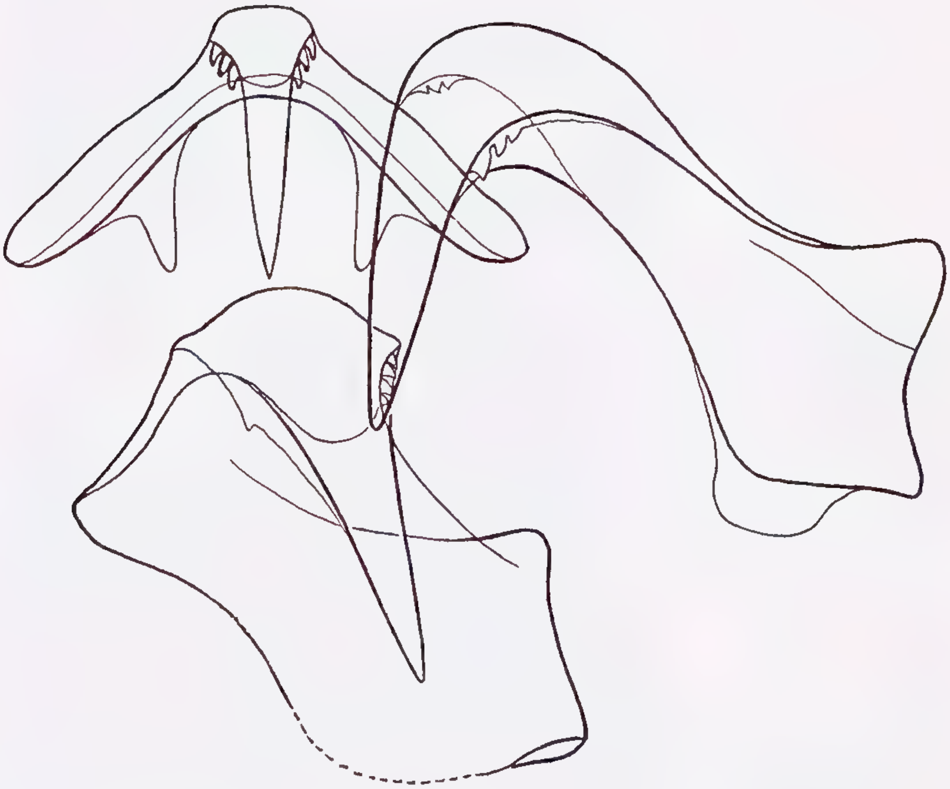

**Fig. 3.** *Tutufa (Tutufella) rubeta* (Linnaeus), central and lateral teeth from one half row of radula in normal resting postion, plus (lower sketch) lateral tooth turned half outwards; m.v. "Pele" Mariel King Memorial Exped. stn. CP.II, Piru Bay, Ceram, Moluccas; WAM.

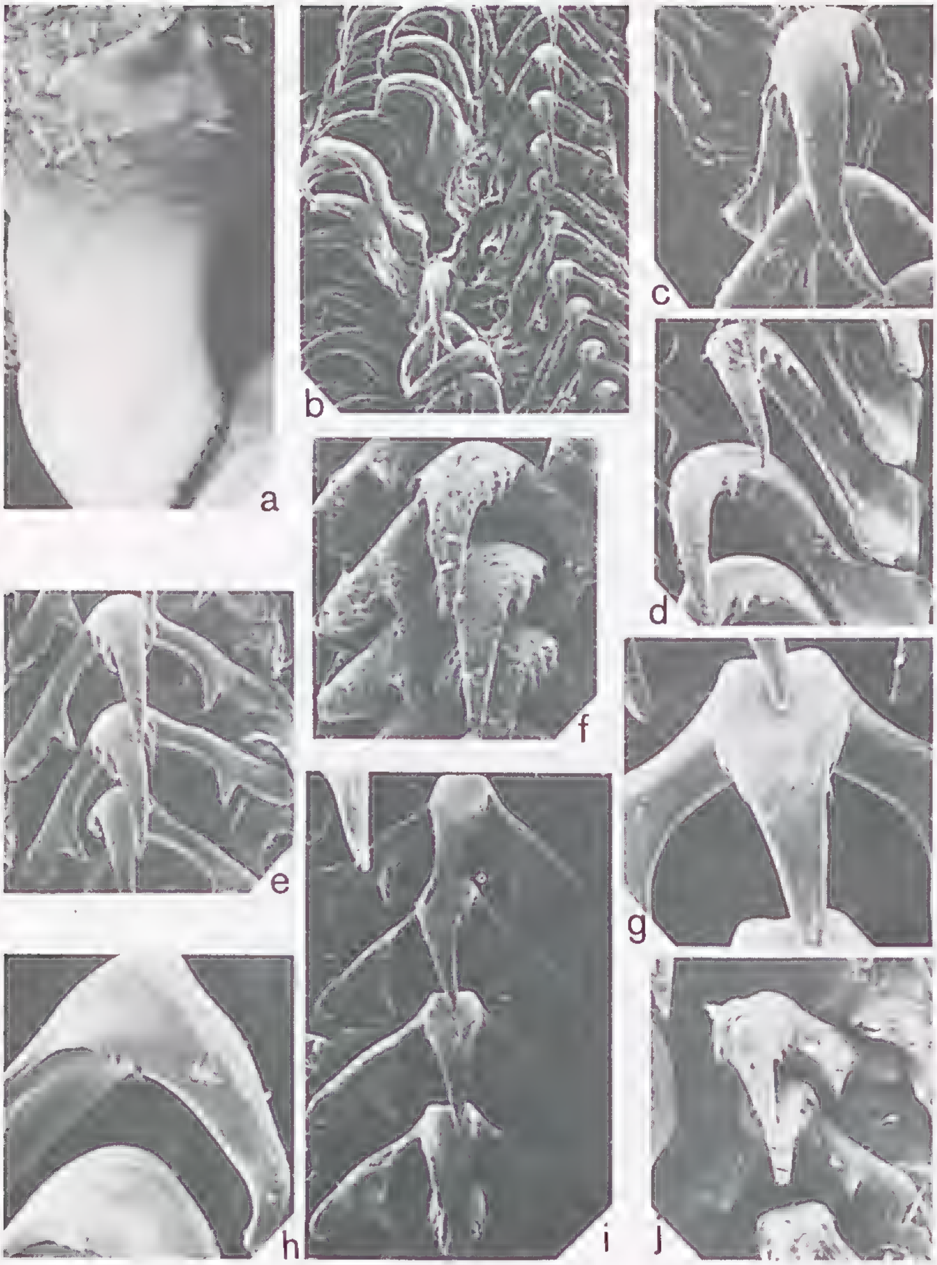

**Fig. 4 a.** *Tutufa (Tutufa) bubo* (Linnaeus), neotype, and lectotype of *Bursa rubeta* var. *gigantea* E. A. Smith, columellar sculpture (turned 30° to left); the similar *T. bardeyi* has a smooth columella. BMNH 1899.12.27.8 (X 0.6). **b-j.** Scanning electron micrographs of radulae of *Tutufa* and *Bursa (Bufonariella)*. **b.** *Tutufa (Tutufella) oyamai* Habe, general view of undisturbed central teeth and displaced left lateral and marginal teeth, X 90; m.v. "Pele" Mariel King Memorial Exped. sta. KR VI/3-10, Kai I., Moluccas (WAM). **c.** Left lateral tooth of same radula as in Fig. 4b, turned half outwards, X 285. **d.** Right lateral teeth of same radula as in Fig. 4b, in normal rest postion, X 215. **e.** Central teeth of same radula as in Fig. 4b, X 215. **f.** *Tutufa (Tutufella) oyamai* Habe, central teeth of larger specimen than in Fig. 4b (poorly cleaned), X 220; m.v. "Pele" Mariel King Memorial Exped. Sta. ANI/1, Aru I., Moluccas; WAM (drawn in Fig. 2e). **g.** *Tutufa (Tutufella) rubeta* (Linnaeus), main cusp of central tooth, X 220; m.v. "Pele" Mariel King Memorial Exped. Sta. CP II, Piru Bay, Ceram; WAM (drawn in Fig. 3) **h.** Cusp of left lateral tooth of same radula as in Fig. 4g, X 180 (scratches are artifical). **i.** Portion of row of central teeth of same radula as in Fig. 4g, X 95. **j.** *Bursa (Bufonariella) ranelloides humilis* n. subsp., paratype, central teeth of radula (poorly cleaned), X 140; H.M.A.S. "Diamantina" Sta.6, N.W. of Bunbury, Western Australia; WAM 305-72 (drawn in Fig. 2b).

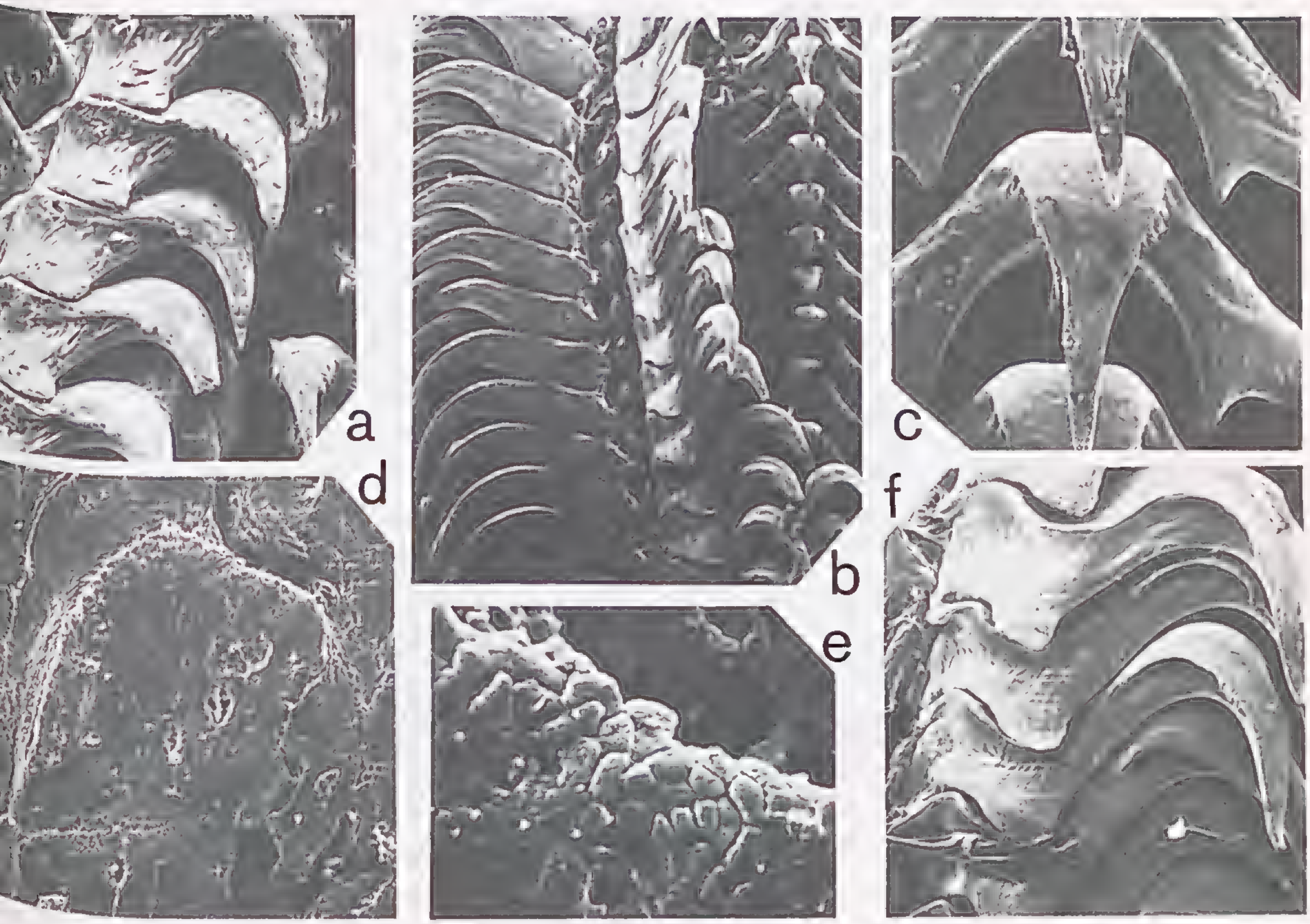

**Fig. 5** Scaning electron micrographs of *Tutufa* radulae and jaw plates. **a.** Left lateral teeth of same radula as in Fig. 4j, X 75. **b.** *Tutufa (Tutufa) bufo* (Röding), general view of little-disturbed radula showing interlocked teeth, X 20; off Osbourne Shoals, Bate Bay, Cronulla, New South Wales; AM, C 73465 (drawn in Fig. 2c). **c.** Main cusps of central teeth of same radula as in Fig. 5b, X 90. **f.** Left lateral teeth of same radula as in Fig. 5b, showing interlocked bases, X 70. **d, e.** *Tutufa (Tutufella) rubeta* (Linnaeus), jaw plate, attached to section of "lip" epidermis; m.v. "Pele" Mariel King Memorial Exped. sta. CP II, Piru Bay, Ceram; WAM. **d.** anterior half of damaged plate, X 140; **e.** platelets of central anterior edge, X 690.

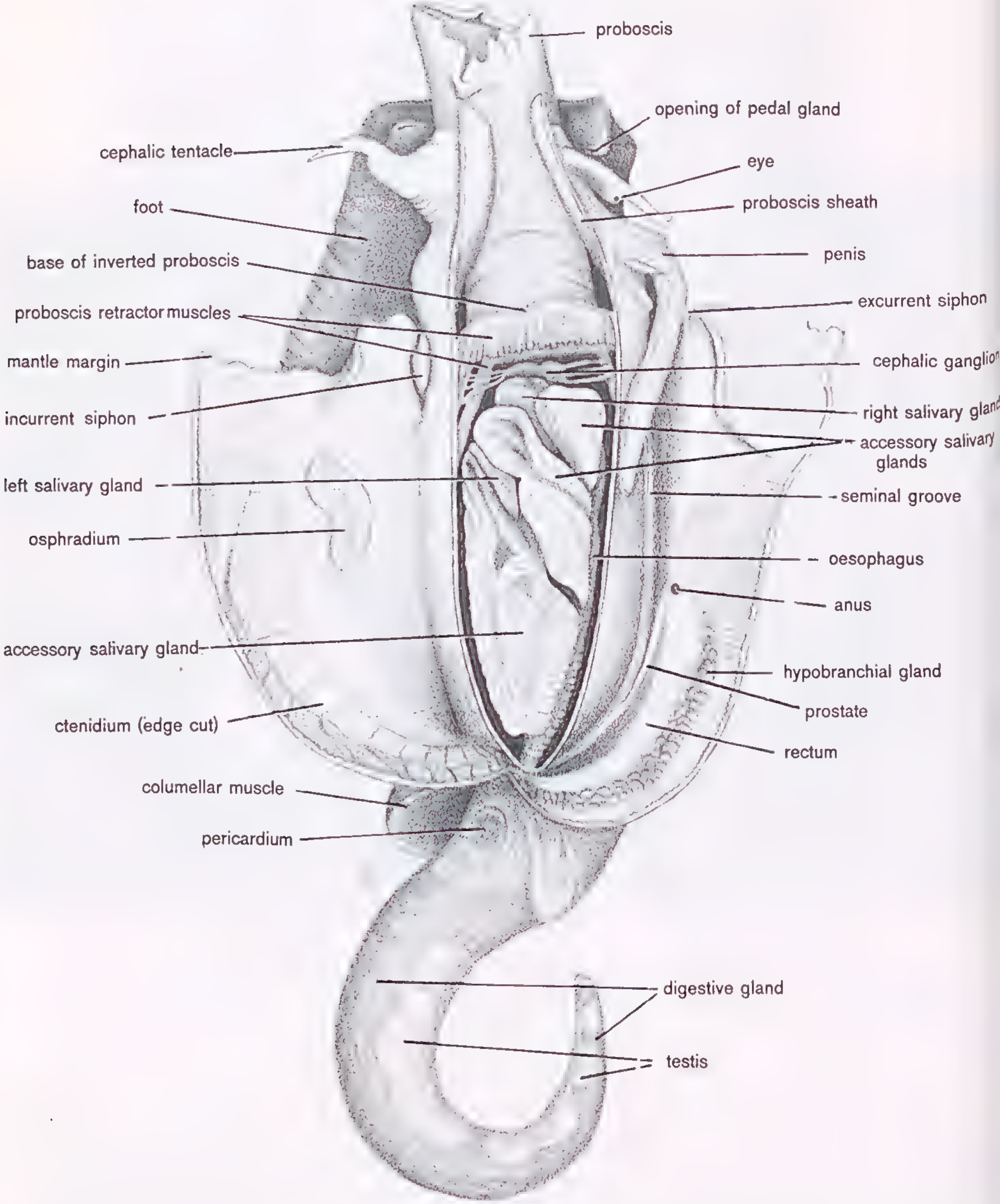

**Fig. 6.** *Tutufa (Tutufa) bubo* (Röding), sketch of gross anatomy of mantle and cephalic cavities. Length of whole animal in position shown is approx. 13 cm. Off Osbourne Shoals, Bate Bay, Cronulla, N.S.W., 30 m; AM, C 73465.

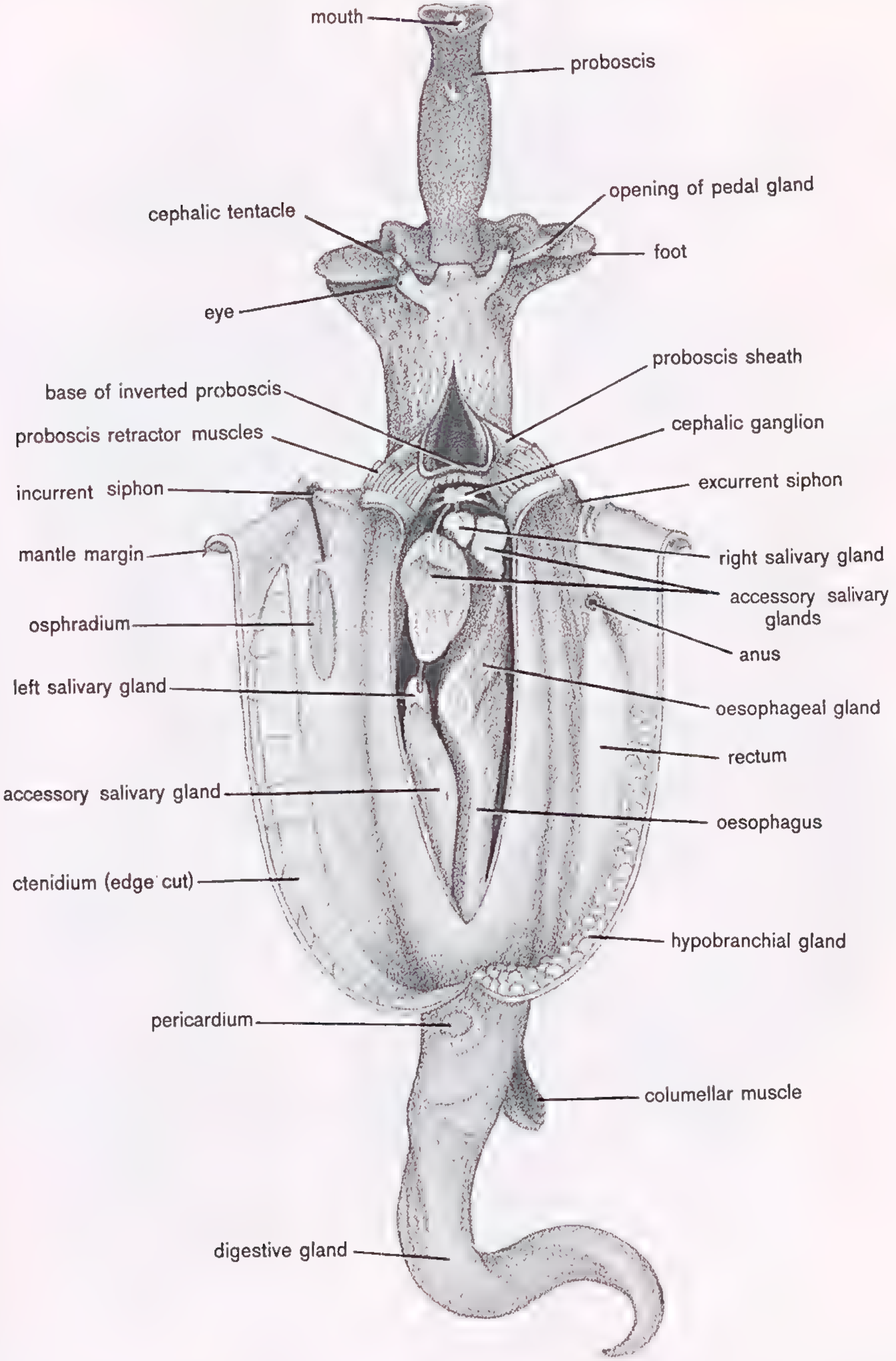

Fig. 7. *Tutufa (Tutufella) rubeta* (Linnaeus), sketch of gross anatomy of mantle and cephalic cavities (approx. X 1.5); m.v. "Pele" Mariel King Memorial Exped. stn. CP II, Piru Bay, Ceram, Moluccas; WAM.

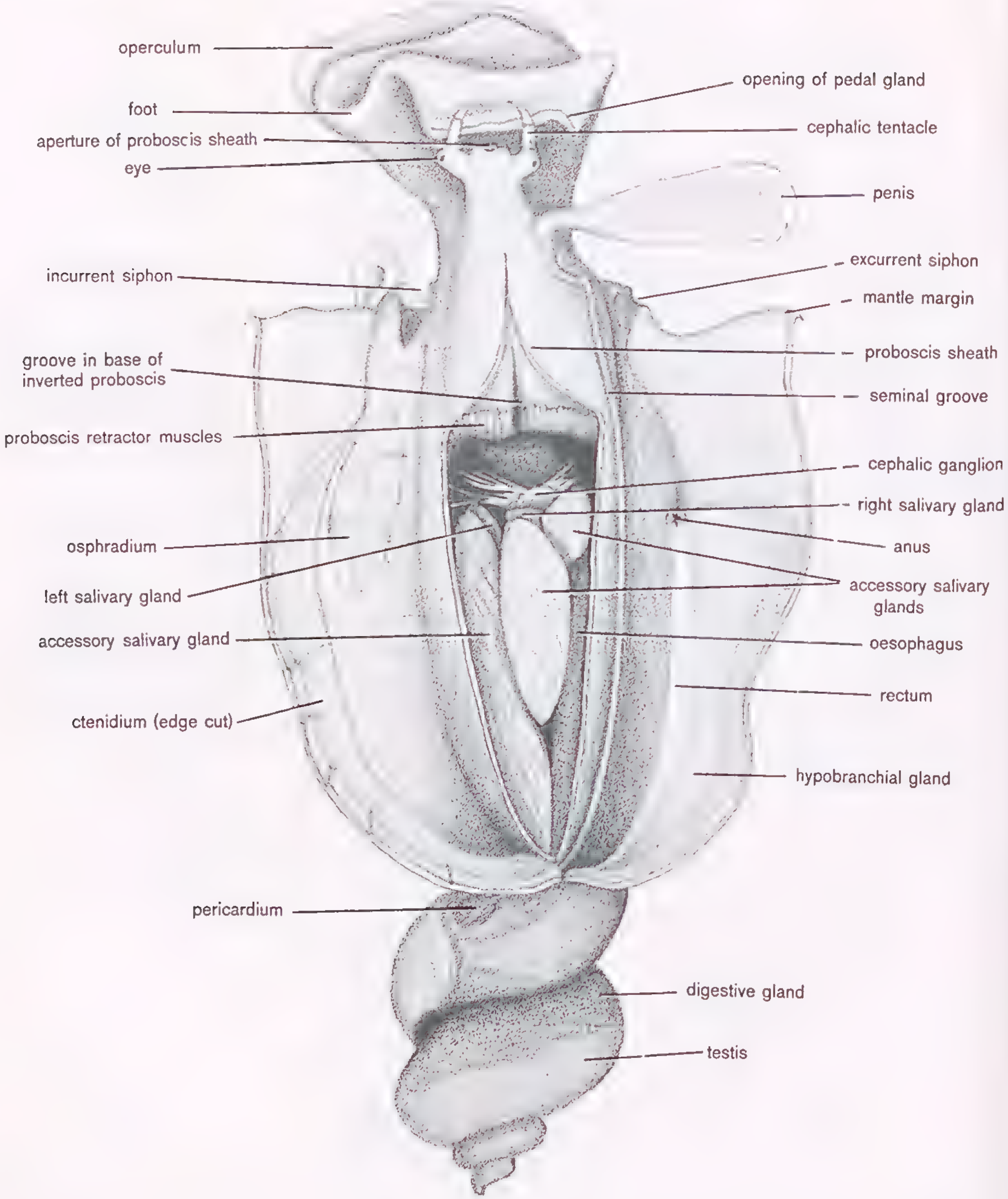

**Fig. 8.** *Bursa (Bufonariella) ranelloides humilis* n.subsp., paratype, sketch of gross anatomy of mantle and cephalic cavities (approx. X 4). H.M.A.S. "Diamantina" stn. 6, N.W. of Bunbury, Western Australia, 212-226 m; WAM 305-72.

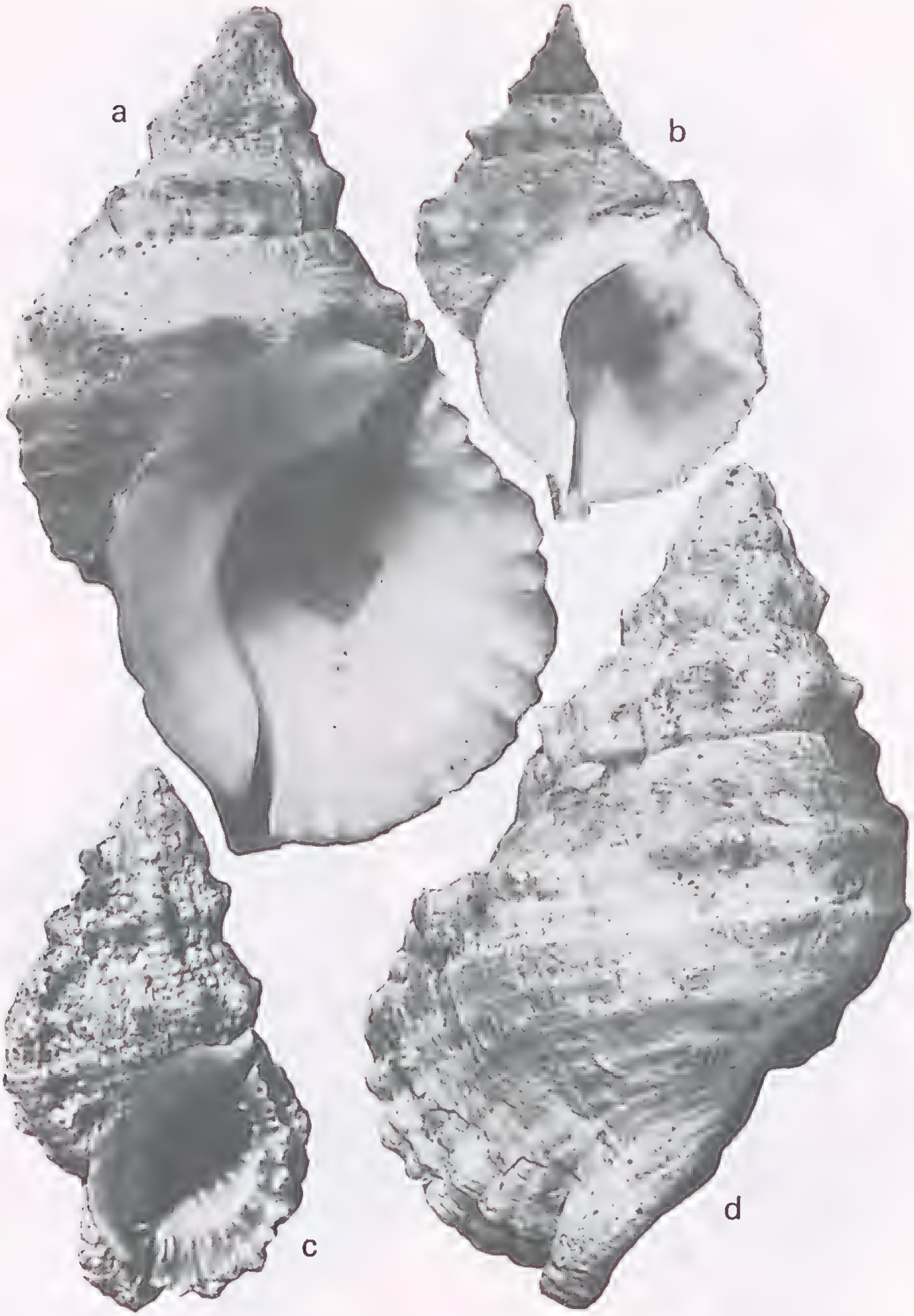

**Fig. 9. a,b,d,** *Tutufa (Tutufa) bardeyi* (Jousseaume). **a,d.** Paralectotype of *Bursa (Tutufa) rubeta* var. *gigantea* E. A. Smith, 1914, figured by Smith (1914, pl. 4, fig. 5), Muscat, Oman; BMNH 1899.12.27.8 (X 0.33). **b.** Previously unfigured paralectotype of *Bursa (Tutufa) rubeta* var. *gigantea* E. A. Smith, 1914, Muscat, Oman; BMNH 1899.12.27.9 (X 0.25). **c.** *Tutufa (Tutufella) rubeta* (Linnaeus, 1758), Port Moresby, New Guinea; NZNM, MF 21548, X1.

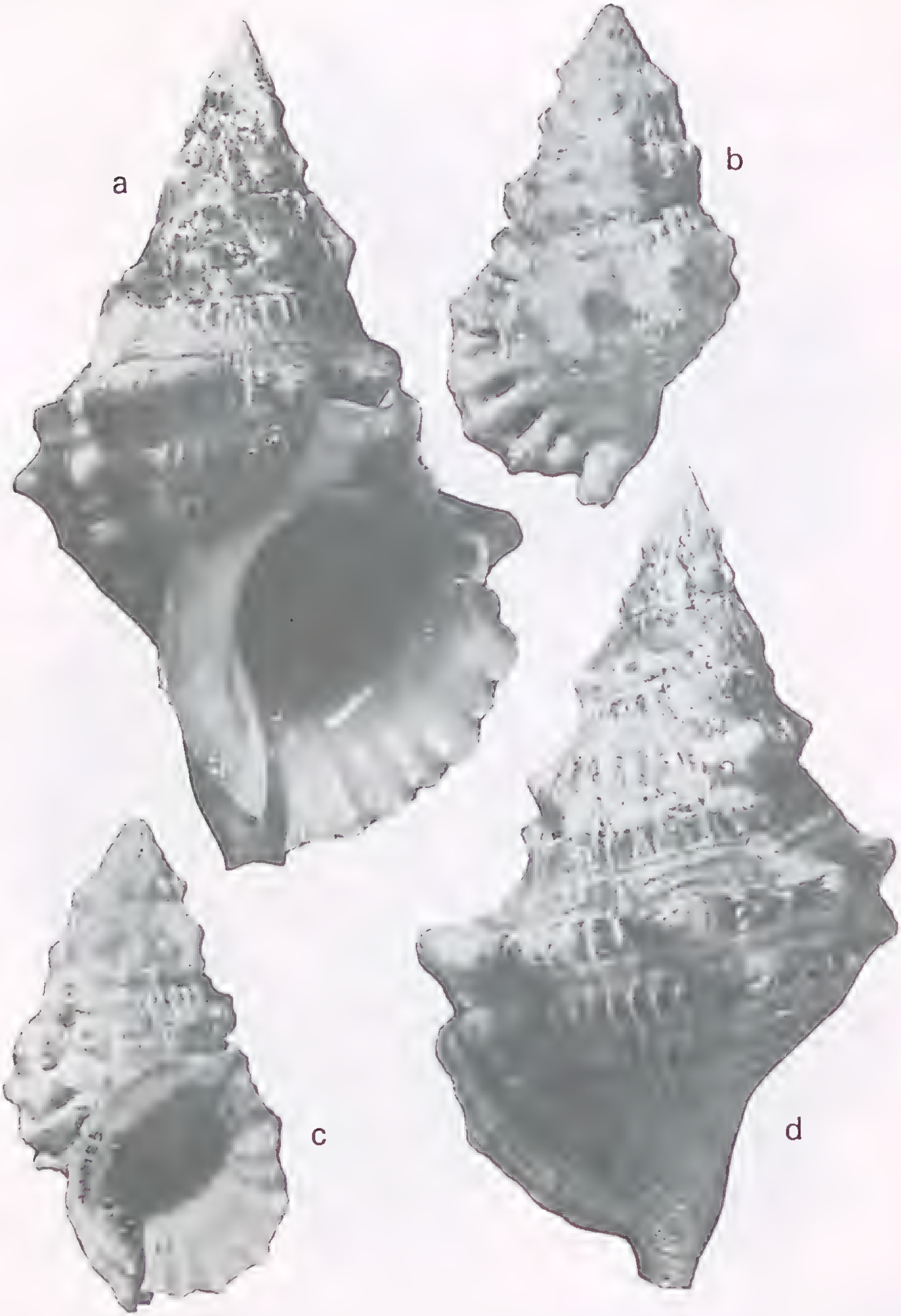

**Fig. 10. a,d** *Tutufa (Tutufa) bardeyi* (Jousseaume, 1894), Bir Ali and Mukalla, East Aden Protectorate; WAM, X 0.5. **b,c.** *Tutufa (Tutufella) cf. rubeta* (Linnaeus), pale specimen with dark inner lip, Moçambique Island, Moçambique; NM, G 3444 (X1.)

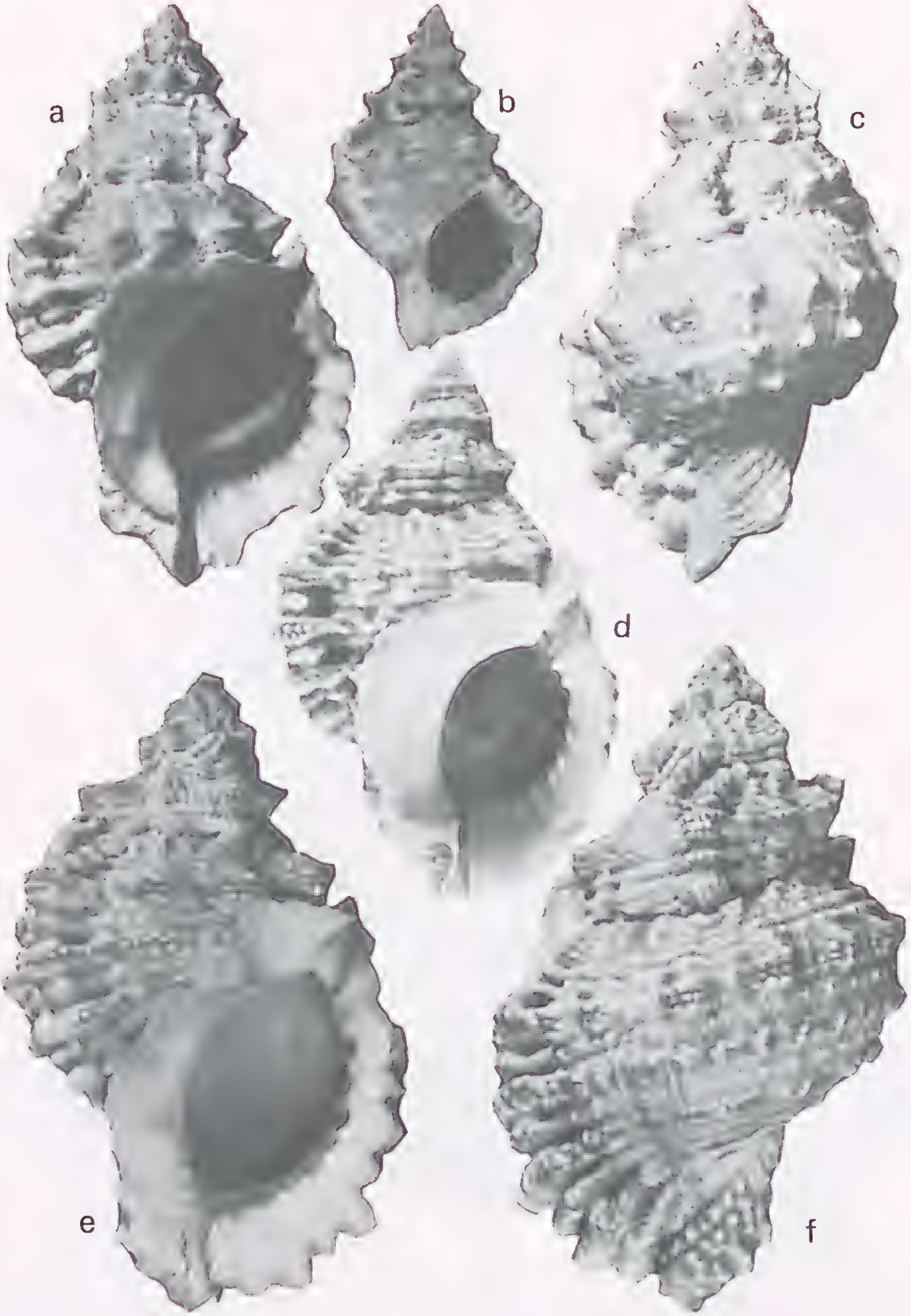

**Fig. 11. a, c-f** *Tutufa (Tutufa) bufo* (Röding, 1798). **a, c.** 130-160 m, off Wedge I., central Western Australia; NZGS, WM 10744 (X 0.66). **d.** lectotype of *Bursa (Tutufa) rubeta* var. *lissostoma* E. A. Smith, 1914, unlocalised; BMNH 197384 (X 0.8). **e,f.** Townsville, Queensland; AM, C 66562 (X1). **b.** *Tutufa (Tutufa) bubo* (Linnaeus, 1758) juvenile, specimen recorded as *"Bursa lampas"* by E. A. Smith (1906), Durban Bluff, South Africa; BMNH 1906.7.7.6 (enlarged X 1.6).

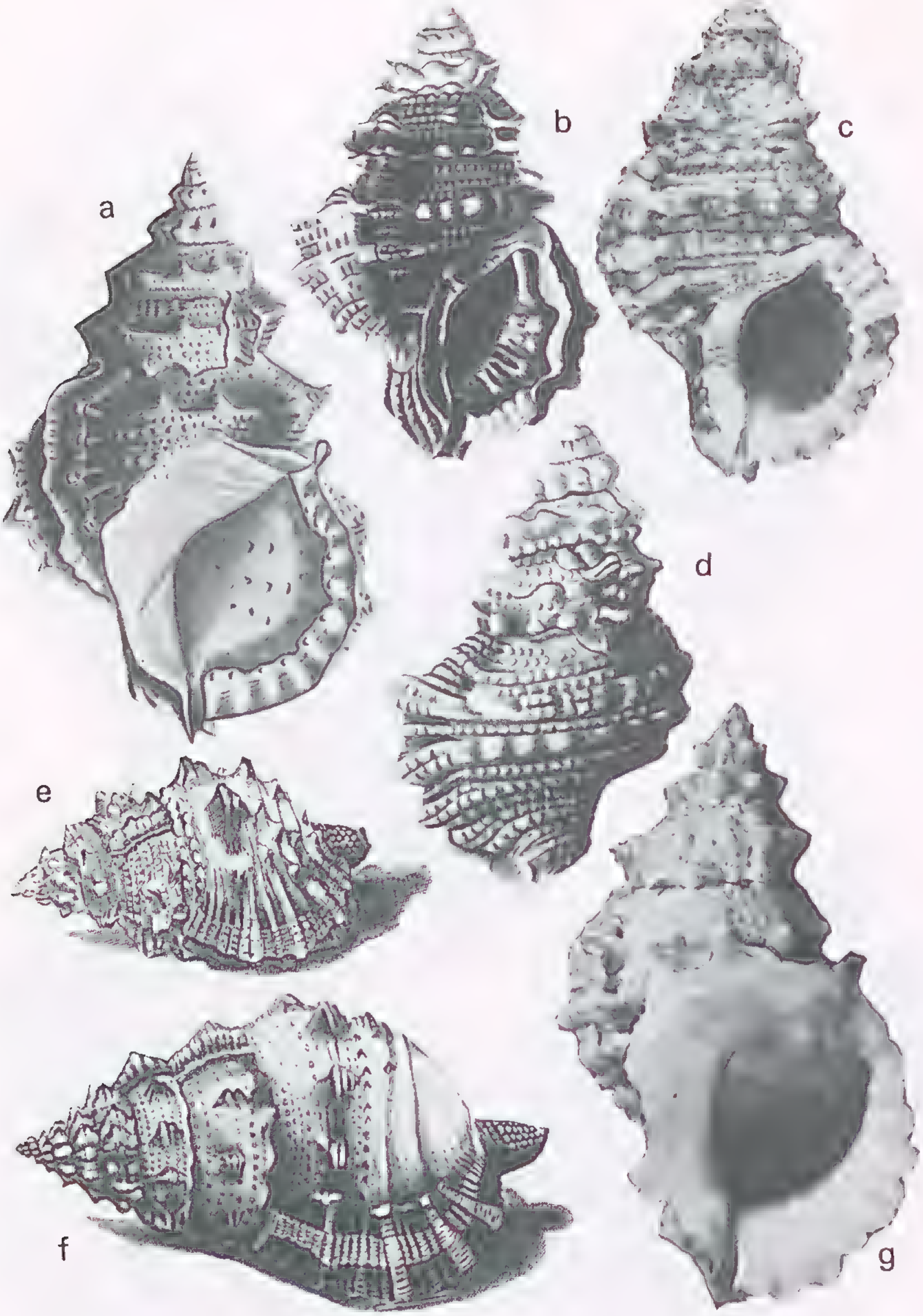

**Fig. 12. a** *Tutufa (Tutufa) bufo* (Röding, 1798), copy of Martini's (1780, pl. 129, fig. 1238) figure cited for *Tritonium bufo* by Röding (1798, p. 128), reduced to X 0.5. **b-e.** *Tutufa (Tutufella) rubeta* (Linnaeus, 1758). **b,d.** — copy of Martini's (1780, pl. 128, fig. 1236, 1237) figure cited for *Tritonium tuberosum* by Röding (1798, p.127), X1. **c.** — locality?; specimen recorded from "Port Natal" by E. A. Smith (1914); BMNH 1861.7.3.29 (X 0.94). **e.** — copy of Rumphius' (1711, pl.28, fig. D) figure cited for both *Murex rana* var. *rubeta* Linnaeus, 1758, and *Tritonium rubeta* Röding, 1798 (X1). **f.** *Tutufa (Tutuba) bubo* (Linneaus, 1758), copy of Rumphius' (1711, pl. 28, fig.C) figure cited for *Murex rana* var. *bubo* Linnaeus, 1758 (X 0.66). **g.** *Tutufa (Tutufa) bufo* (Röding, 1798), off Port Macquarie, New South Wales; AM (X 0.66).

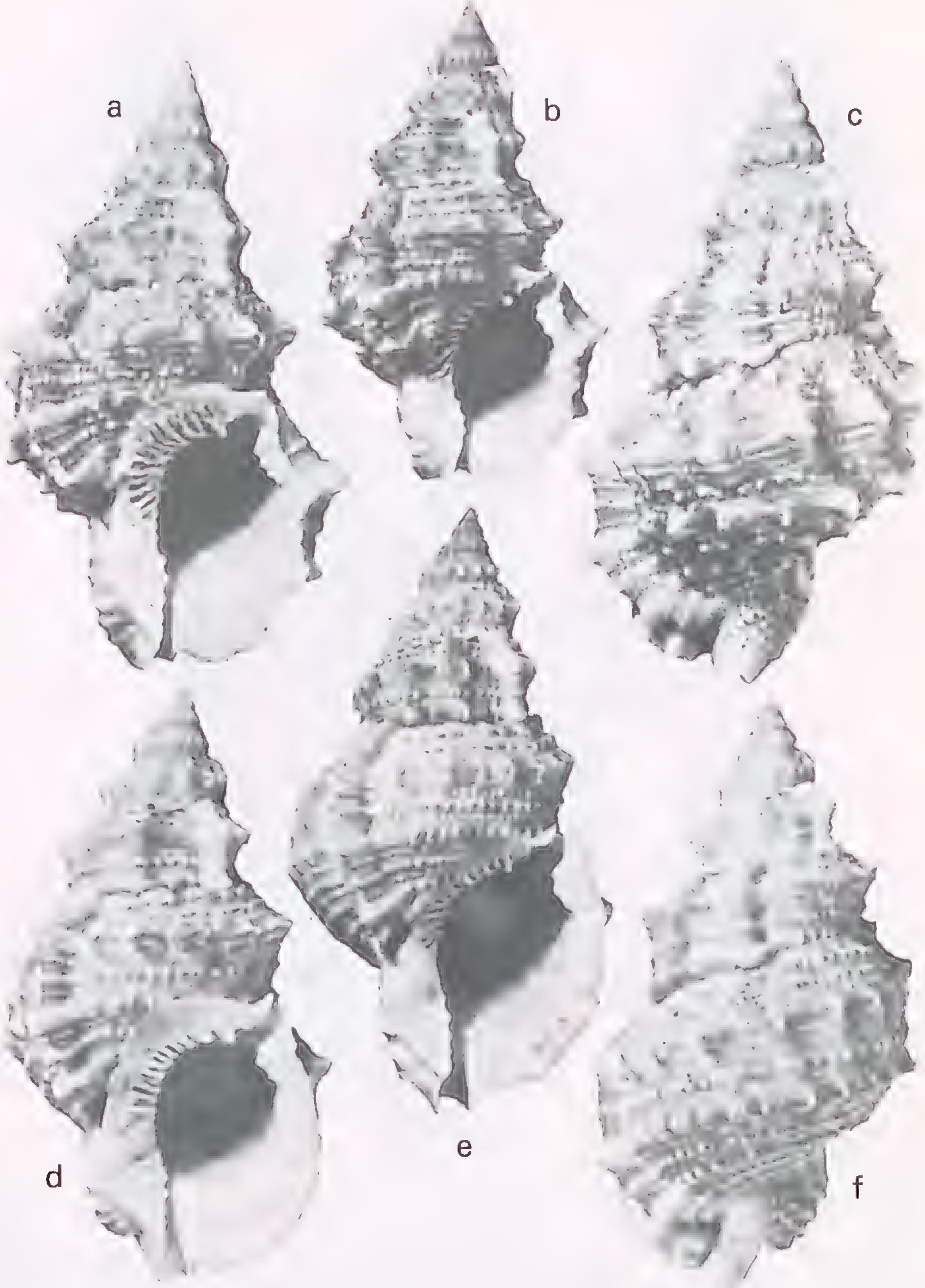

**Fig. 17.** *Bursa (Bufonariella) latitudo wolfei* n. subsp., Hawaii, all X1. **a,c.** — Holotype, crab trap in 58 m, off Makaha, Oahu; Bernice P. Bishop Museum, BPBM 8936. **b.** — paratype, crab trap in 120 m, off Haleiwa, Oahu; C. S. Wolfe Colln. **d, f.** — paratype, 120 m, of Kahuku, Oahu; C. S. Wolfe Colln. **e.** — paratype, locality as Fig. 15 d, f; S. Handrahan Colln.

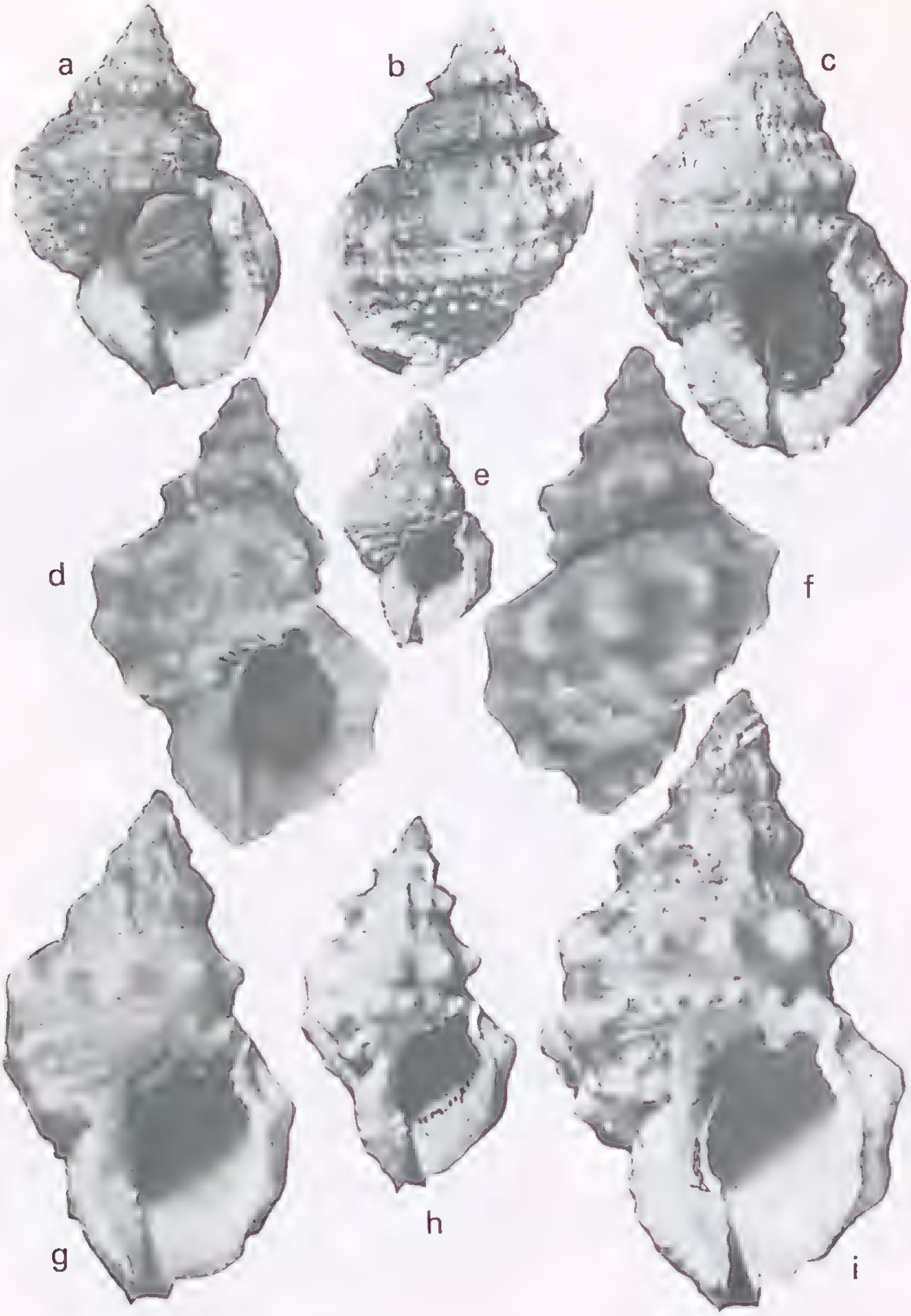

**Fig. 18. a-c, e.** *Bursa (Bufonariella) ranelloides humilis* n. subsp., Western Australia, all X 1.5. **a,b.** — holotype, H.M.A.S. "Diamantina" stn. 6, NW of Bunbury, 212-226 m; WAM 505-72. **c.** — paratype, H.M.A.S. "Diamantina" stn. 25, NW of Bunbury, 161-165 m WAM 310-72. **e.** — juvenile paratype, H.M.A.S. "Diamantina" stn. 19, W of Cape Hamelin, 190-161 m; WAM 309-72. **d, f-i.** *Bursa (Bufonariella) ranelloides ranelloides* (Reeve, 1844), Japan. **d., f.** — holotype, "Matnog, Province of Albay, Luzon, Philippine Islands" (really from southern Japan); BMNH 1967594 (X 1.44; height = 49.65 mm). **g.** — 90 m, Tosa Bay, Shikoku, weakly noduled specimen; NZNM, MF 5558 (X 1.5). **h** — Tosa Bay, Shikoku; NZGS, WM 11277 (X1), **i.** — 35 m, Tosa Bay, Shikoku, the common large-noduled form; NZNM, MF 5559 (X 1.5).

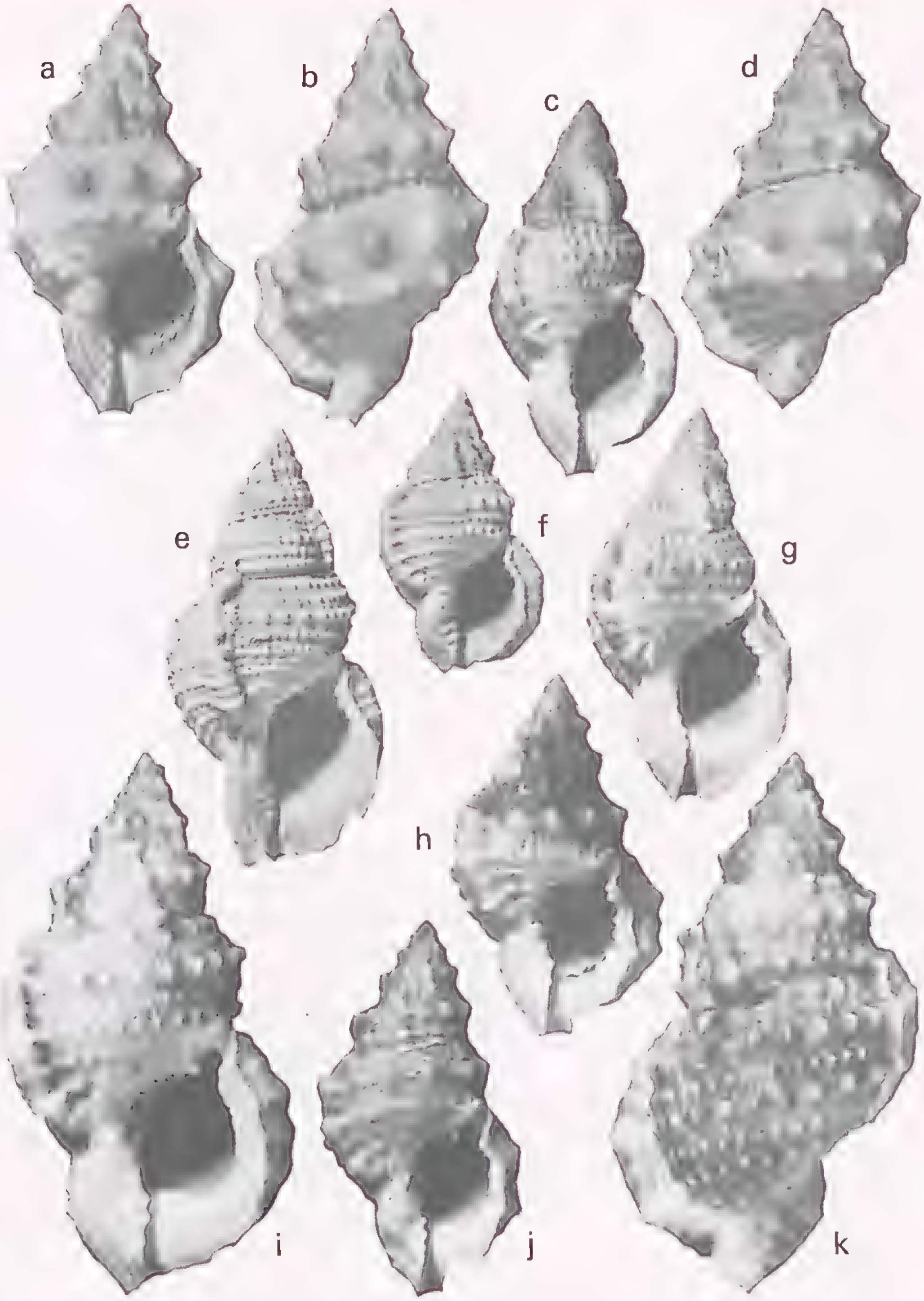

**Fig. 19.** *Bursa (Bufonariella) ranelloides tenuisculpta* Dautzenberg & Fischer, 1906. **a,b.** Holotype of *Bursa finlayi* McGinty, 1962, 210 m, off Sombrero Key Light, middle Florida Keys, "Triton" stn. 615; USNM 634570 (X 1.5). **c,g.** 230 m, Dry Tortugas, Florida; C. S. Wolfe Colln. (X1). **d.** — N of Virgin Islands, 180-550 m; USNM 430336 (X 1.5). **e.** — "Eolis" stn. 146, 180 m, off Key West, Florida; USNM 41778 (X1). **f.** — State Univ. Iowa dredging stn. 29, Bahia Honda, Cuba; USNM 543506 (X1). **h, j.** — off mouth of Tugela River, Natal, South Africa, 32 m, Nov. 1972; Natal Museum, A12 (X 1.5). **i,k.** — 275 m, SE of Durban Bluff, South Africa, Aug. 1972; Natal Museum, 9928 (X 1.5).

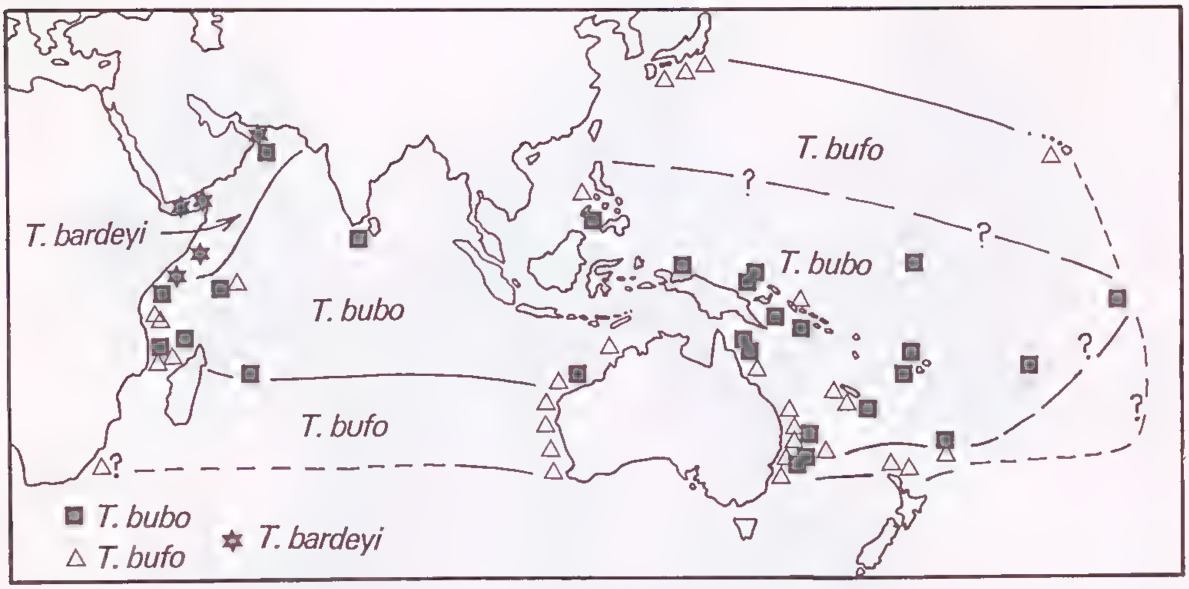

**Fig. 20.** Distribution of species of *Tutufa (Tutufa)*, based on published records and on the collection of the Australian Museum.

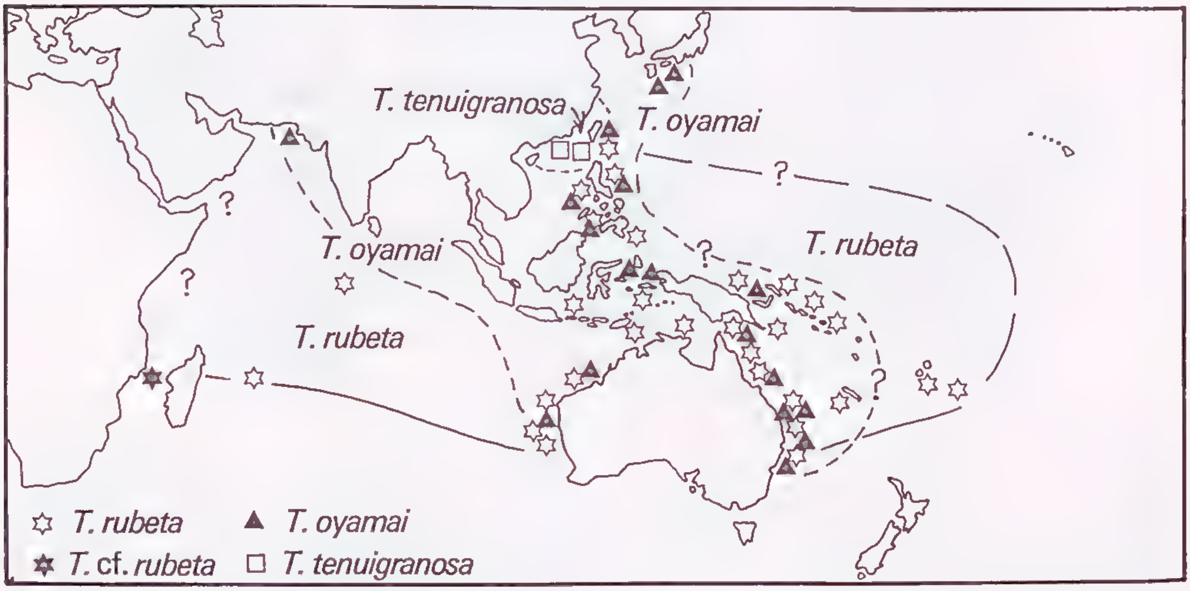

**Fig. 21.** Distribution of *Tutufa (Tutufella)*, based on published records and on the collection of the Australian Museum.

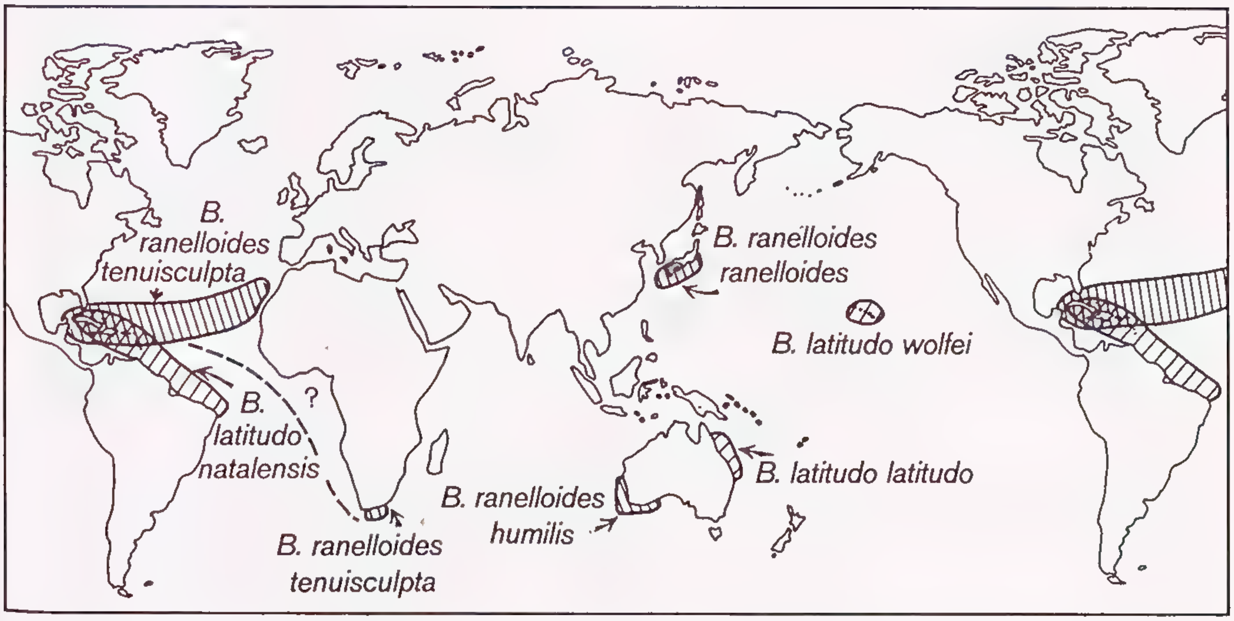

**Fig. 22.** Distribution of subspecies of *Bursa (Bufonariella) latitudo* and *B. (Bufonariella) ranelloides*.

# A SEA ANEMONE, *EDWARDSIA MERIDIONALIS* SP. NOV., FROM ANTARCTICA AND A PRELIMINARY REVISION OF THE GENUS *EDWARDSIA* DE QUATREFAGES, 1841 (COELENTERATA: ACTINIARIA).

NATIONAL MUSEUM
-9 APR 1981
OF VICTORIA

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## SUMMARY

A newly recognized sea anemone, *Edwardsia meridionalis* sp. nov., from McMurdo Sound, Antarctica is described and compared with other *Edwardsia* species. Its habitat and geographical distribution are described.

The generic name *Edwardsia* de Quatrefages, 1841 and the familial name Edwardsiidae Andres, 1881 are invalid. A summary of a proposal made to the International Commission on Zoological Nomenclature to conserve these names is given.

The genus *Edwardsia* is defined and its known synonyms are given. A review of the published descriptions found of nominal *Edwardsia* species revealed many *nomina nuda*, *nomina dubia*, synonyms and homonyms. The remaining *nomina clara* comprize forty currently accepted nominal species, which are listed with their known synonyms and geographical distributions.

The following nomenclatural changes are instituted: *E. carlgreni* nom. nov. is proposed as a replacement name for *E. pallida* Carlgren, 1921, a junior primary homonym of *E. pallida* Verrill, 1879; *E. neozelanica* Farquhar, 1898, a subjective synonym of *E. elegans* Farquhar, 1898, is proposed as a replacement name for *E. elegans* Farquhar, which is a junior primary homonym of *E. elegans* Verrill, 1869; *E. claparedii* (Panceri, 1869) is regarded as the valid name of *E. callimorpha* (Gosse, 1853) (*sensu* Stephenson, 1935) whilst *E. callimorpha* (Gosse, 1853) (*sensu stricto*) reverts to *Scolanthus callimorphus* Gosse, 1853; *E. perdita* nom. nov. is proposed as a replacement name for *E. grubii* Andres, 1883, a junior secondary homonym of *E. grubii* (A. Costa, 1869); *Fagesia janthina* comb. nov. is proposed for *E. janthina* Andres, 1881; *E. horstii* Pax, 1924b is a simultaneously published synonym of *Isoedwardsia curacaoensis* Pax, 1924b and its valid name is here regarded as *Scolanthus curacaoensis* (Pax, 1924b).

Further research may reveal invalid names amongst the currently accepted nominal species: notes are made on some of those which might prove to be invalid. Furthermore, any of the *nomina dubia* might be raised to the status of *nomina clara* if type material were found, but their validity would still remain to be established.

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## INTRODUCTION

The coelenterate genus *Edwardsia* de Quatrefages, 1841 is one of the largest known within the order Actiniaria (sea anemones) and its distribution is world wide: all members of the genus burrow into mud, sand or gravel. It is a curious fact that although Actiniaria have frequently been collected from McMurdo Sound in Antarctica, no species of *Edwardsia* have hitherto been reported there. However, during studies on the diversity and structure of benthic communities in the Sound, large numbers of an un-named *Edwardsia* species were collected in 1970 by Dr J. K. Lowry (then at the University of Canterbury, Christchurch, New Zealand; currently at the Australian Museum, Sydney). Through the kindness of Dr Lowry and Mr J. S. Oliver in supplying specimens I have been able to make the following description of the species for which I propose the name *Edwardsia meridionalis* sp. nov.: the trivial name refers to its southerly distribution.

Carlgren (1949), in a survey of the world's sea anemones, listed 55 species of *Edwardsia* which he apparently regarded as valid and several more have since been described. An examination of the original and some subsequent descriptions of these and all the other nominal species of *Edwardsia* which were found in the literature revealed the need for a review of the genus. The number of presently accepted species is reduced to forty and the remaining nominal species are classified as *nomina nuda, nomina dubia,* synonyms or homonyms. It should be emphasized that some of the presently accepted nominal species listed in appendix II might prove to be conspecific: some of the possible synonyms are noted, but further research is necessary to assess their status. Furthermore, any of the *nomina dubia* might be raised to the status of *nomina clara* if type material were found but their validity would still remain to be established.

## SYSTEMATICS: DESCRIPTION OF *EDWARDSIA MERIDIONALIS* SP. NOV.

### **Edwardsia** de Quatrefages, 1841*, p.427

*Edwardsia.* — de Quatrefages, 1842, p.68; Carlgren, 1921, p.27; Stephenson, 1935, p.52; Carlgren, 1949, p.22; Manuel, 1977, p.484.

*Actinia.* — Stimpson, 1853, p.7 *(pro parte);* [*non Actinia* Browne, 1756, = *Actinia auct.*, *e.g.* Stephenson, 1935†].

*Milnea.* — Reichenbach *in* Wright, 1866, p.782; (see appendix I).

*Urophysalus.* — A. Costa, 1869, p.56; (see below).

*Halcampa.* — Panceri, 1869, p.6 *(pro parte).*

*Edwardsiella.* — Andres, 1883, p.305 *(pro parte)*; McMurrich, 1913, p.551; Verrill, 1928, p.27.

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* The usage of this genus-group name which is preoccupied by *Edwardsia* O. G. Costa, 1834, is discussed in appendix I. No nominal species were included at the time the genus was established.

† *Actinia* Browne, 1756, being published before the starting point of zoological nomenclature, is an unavailable name: the valid name of this genus is *Priapus* Linnaeus, 1758.

*Diphtera*‡. — Sluiter, 1888, p.233; Sluiter, 1889, p.47; (see below.)

*Edwardsioides*. — Danielssen, 1890, p.100.

REMARKS. The name *Scolanthus* Gosse, 1853, p.157, has long been considered to be a junior synonym of *Edwardsia* de Quatrefages, 1841 (see Gosse, 1855a; Haddon, 1889; Stephenson, 1935.) Hence *Scolanthus callimorphus* Gosse, 1853 has been known for over a century as *Edwardsia callimorpha* (Gosse, 1853) (see Stephenson, 1935.) However, it has recently been found that *S. callimorphus* Gosse, 1853 is synonymous with *Isoedwardsia (Edwardsia) lucifuga* (Fischer, 1888) (Manuel, in preparation). *Scolanthus* Gosse, 1853 is therefore a senior subjective synonym of *Isoedwardsia* Carlgren, 1921 and the latter name is here regarded as invalid: for this reason, *Scolanthus* is no longer regarded as a synonym of *Edwardsia*. (However, *Scolanthus* (*sensu* Holdsworth, 1855, p.85) is a synonym of *Sagartia* Gosse, 1855a, p.272.) The valid name of *E. callimorpha* (*sensu* Stephenson, 1935) is here considered to be *E. claparedii* (Panceri, 1869) (*q.v.*), with which Mr Manuel concurs.

*Lecythia* Sars, 1829, p.27, was synonymized by implication with *Edwardsiella* Andres, 1883 by Andres (1883) and by Delage and Hérouard (1901) because the type-species by monotypy, *L. brevicornis* Sars, 1829 was synonymized doubtfully by Andres (1883) with *Edwardsia (Edwardsiella) sarsii* Düben and Koren, 1847. Although Carlgren (1921) subsequently synonymized *L. brevicornis* with *Paraedwardsia sarsii* (Düben and Koren, 1847) and furthermore, used the morphological data of Sars (1829) to add to his own description of *P. sarsii*, it is clear from his text that he really regarded *Lecythia* Sars, 1829 as a *nomen dubium*. If this were not the case the name *Lecythia* Sars, 1829 would have had priority over *Paraedwardsia* Carlgren, 1905. *Lecythia* is regarded here also as a *nomen dubium* and is therefore not synonymized with either *Edwardsia (Edwardsiella)* or *Paraedwardsia*.

Although *Urophysalus* A. Costa, 1869 is synonymized here with *Edwardsia*, as it was by Andres (1883), the only included species (*U. grubii, q.v.*), which Andres (1883) considered to be synonymous with *E. claparedii* (Panceri, 1869) is here regarded as a *nomen dubium*. Similarly, the type-species by monotypy (*D. octoplax, q.v.*) of *Diphtera* Sluiter, 1888 is here regarded as a *nomen dubium* although *Diphtera* is clearly a synonym of *Edwardsia*.

The generic definition of *Edwardsia* de Quatrefages, 1841 given below is that of Manuel (1977) which is based on that of Carlgren (1949).

"Edwardsiidae (*sensu* Carlgren, 1949) with column divisible into physa, scapus, scapulus and capitulum. Physa never with periderm (cuticle) or nemathybomes; morphologically and functionally differentiated from the scapus. Scapus long, always with periderm and nemathybomes, the latter being externally opening cavities sunk in the mesogloea which contain nematocyst batteries. Eight perfect mesenteries (macrocnemes) and at least four imperfect ones (microcnemes), the latter very weak and restricted to the most distal part of the column. Gonads, filaments, parietal and retractor muscles on the macrocnemes only. Parietals well developed; retractors strong, diffuse to circumscript-diffuse. Cnidom: spirocysts, basitrichs, microbasic *b*-mastigophores and microbasic *p*-mastigophores."

For general terminology, see Stephenson (1928) and Carlgren (1949). Fig. 1 (a-c) is a diagrammatic representation of the general structure of an *Edwardsia*. Various species

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‡ Mistakenly listed *Diphthera* by Neave (1939) in his *Nomenclator Zoologicus*.

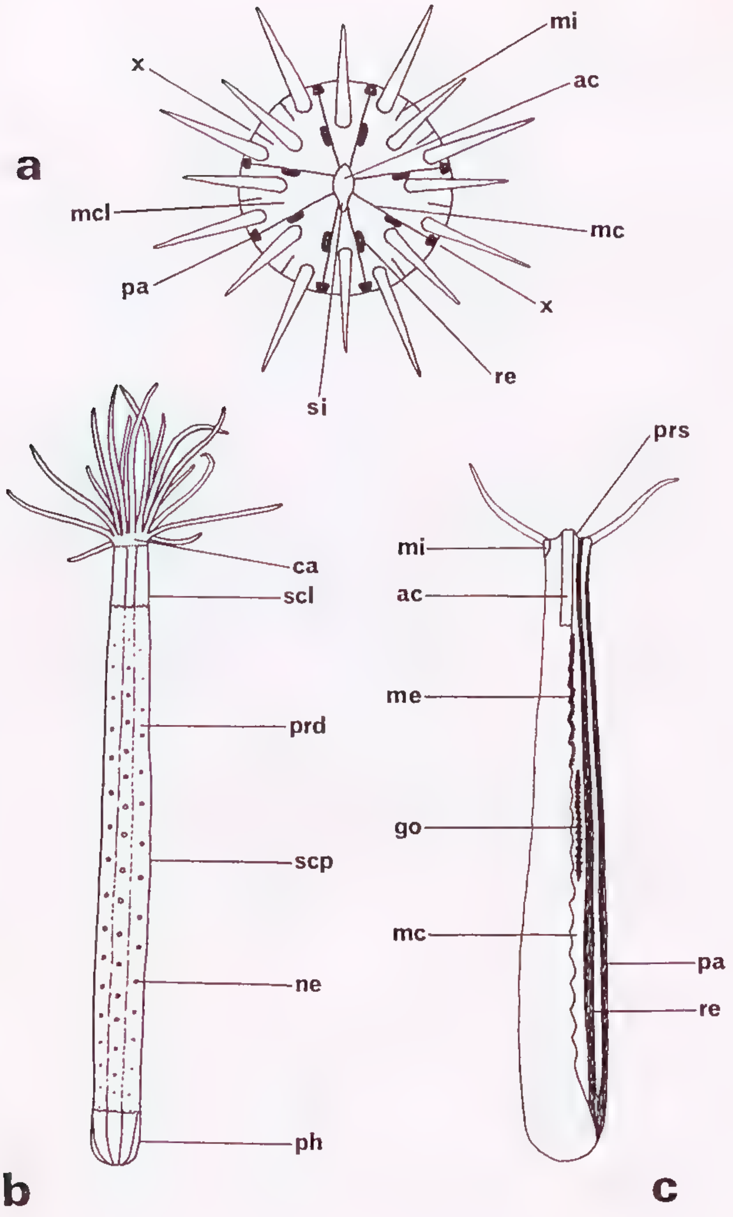

Figure 1. — Schematic diagrams of a generalized *Edwardsia*, to various scales: **(a)** transverse section through capitulum of a species with 16 tentacles (which are superimposed over the mesenteries); **(b)** external features of a whole specimen; **(c)** internal features — a longitudinal section passing through X-X of fig. 1a.
ac = actinopharynx; ca = capitulum; go = gonad; mc = macrocneme; mcl = macrocoel; me = mesenterial filament; mi = microcneme; ne = nemathybomes; pa = parietal muscle; prd = periderm; prs = peristome; ph = physa; re = retractor muscle; scl = scapulus; scp = scapus; si = siphonoglyph.

may differ in detail, particularly in the structure and arrangement of the mesenteries. Cnidae are named according to Weill's (1934) system as modified by Carlgren (1940). Recent research has suggested that basitrichs and *b*-mastigophores may belong to the same category (Westfall, 1965; Schmidt, 1969) but until there is more general agreement amongst researchers on nematocyst nomenclature, it may be better to retain Carlgren's (1940) modification.

### **Edwardsia meridionalis** sp. nov.

Fig. 2a-b

? *E. intermedia.* — Carlgren, 1899, p.6; 1927a, p.4; 1959, p.11 (pro parte(?)); [non McMurrich, 1893, p.136].

*Edwardsia* sp. — Dayton and Oliver, 1977, table 1, p.57.

Definition: *Edwardsia* typically with sixteen white-tipped tentacles in two cycles each of eight, the inner longer than the outer; eight macrocnemes and eight microcnemes. Nemathybomes not visible to the naked eye, concentrated in a band along the centre of each macrocoel, containing microbasic *b*-mastigophores measuring in the region of 29.0-50.7 x 2.6-4.7$\mu$m. Actinopharynx containing microbasic *p*-mastigophores measuring in the region of 14.5-25.9 x 3.6-5.7$\mu$m and two types of microbasic *b*-mastigophores measuring 14.5-23.8 x 1.6-2.6$\mu$m and 35.7-40.3 x 2.6-4.1$\mu$m. Physa imperforate.

TYPE SPECIMENS. The holotype is deposited in the Australian Museum, Sydney; regd no. G.15050; type locality Cape Bird, McMurdo Sound, Antarctica. The following information appears on the label: "*Edwardsia meridionalis* sp. nov.; holotype, dissected. Collected by Dr J. K. Lowry (University of Canterbury, Christchurch, New Zealand) on 28 December, 1970 as part of sample CB2 (depth 65 m) from Cape Bird, Ross Island, McMurdo Sound, Antarctica (77°13'S, 166°25'E). Deposited by Dr R. B. Williams (Tring, England), August 1978." The specimen has 16 tentacles and is 1.2 cm long and 1.5 mm in diameter. The capitulum and scapulus are polygonal , the latter being corrugated, and the physa is slightly puckered at the tip. The colour of the scapus is mainly beige, tan-coloured just above the physa.

Two paratypes are deposited in the British Museum (Natural History), London; regd nos. 1978. 9. 1. 1-2. Three further paratypes (sectioned material) are in the author's private collection.

DESCRIPTION. This is based on examinations of both living and fixed material: the numbers examined are given where appropriate. Measurements of features in living or stained microscopical preparations were made, using an eyepiece micrometer and an oil immersion objective, to an accuracy of ± 0.26$\mu$m after calibration. Measurements are all rounded off to the nearest 0.1$\mu$m. Specimens fixed in 70% alcohol were sectioned at 10 $\mu$m and stained with Masson's Trichrome (Pantin, 1964). The material examined consisted of fixed specimens from Cape Bird (Ross Island, McMurdo Sound) collected by Dr J. K. Lowry, taken from samples CB1 (25 December, 1970) and CB2 (28 December, 1970); and living specimens from Cape Armitage (Ross Island, McMurdo Sound) collected by Mr J. S. Oliver in January, 1976.

Column. Divisible into physa, scapus, scapulus and capitulum, the last being rather indistinct. In fixed, contracted specimens the column was between 4 and 19 mm long and between 0.75 and 2 mm in diameter at its widest point. In living, buried specimens the column was up to 35 mm long and up to 2.5 mm in diameter. It is likely, however, that in relaxed undisturbed specimens, the column may be even longer.

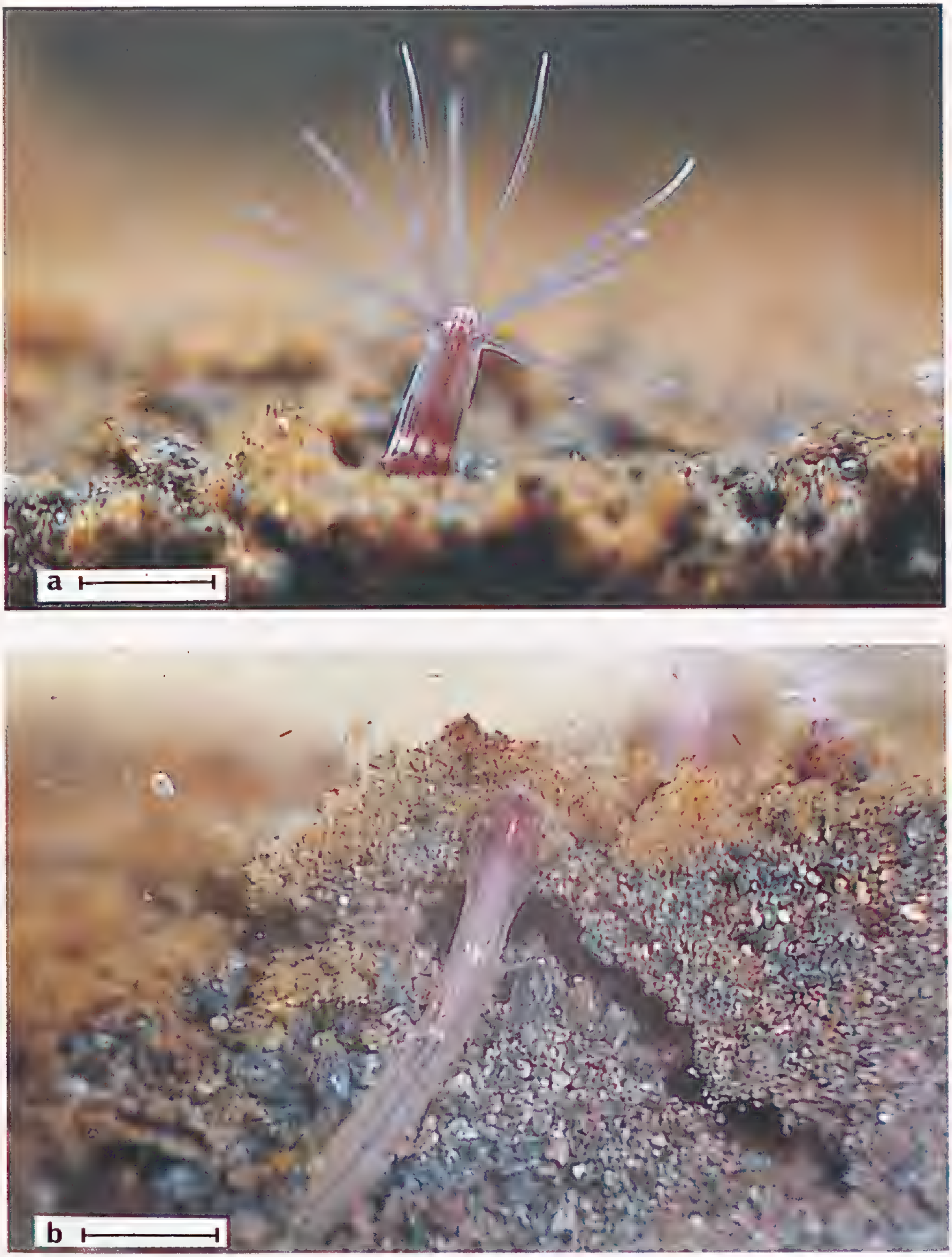

Figure 2. — Photographs of *E. meridionalis* in its natural position in a gravel substrate, viewed through the side of an aquarium (scales = 5 mm): **(a)** expanded at surface; **(b)** tentacles retracted but column still extended below surface.

The physa is translucent when distended, revealing the mesenterial insertions. It is bluish-grey, has no nemathybomes or periderm and is imperforate. Its extremity may become tucked in rosette-like but is not introvertible.

The scapus is corrugated and opaque in contraction, smooth and translucent when extended. The periderm likewise becomes translucent when stretched and ends in a ragged edge where the scapus joins the scapulus distally and the physa proximally. When contracted, the periderm is greyish-brown or ochre, modified by adhering foreign matter, but when stretched, the scapus shows through, being bluish-grey like the physa for most of its length (fig. 2b). The scapus bears non-tuberculate nemathybomes concentrated in a band along the centre of each macrocoel (fig. 3). (The arrangement is similar to that in *E. andresi* but in that species the nemathybomes are relatively smaller (see Carlgren, 1921, fig. 18). For comparison, note the scattered arrangement in *E. norvegica* (see Carlgren, 1942, fig. 68) and an intermediate arrangement in *E. danica* (see Carlgren, 1921, fig. 17).) Nemathybomes in live anemones measured from 39.0 to 58.5$\mu$m across and were not visible to the naked eye in fixed or living material. In transverse sections of the column they were not present at the distal end of the scapus, although periderm was still present at that level. (This could simply have been a result of the column being contracted: fig. 3 was drawn from a live expanded specimen and so represents the nemathybomes in their natural arrangement.)

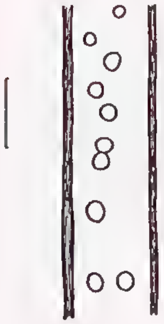

Figure 3. — Distribution of nemathybomes between two mesenterial insertions on the scapus of *E. meridionalis*, 0.7 mm in diameter; scale = 200$\mu$m.

The scapulus has no nemathybomes. Its proximal part is pink or deep chestnut brown: this coloration extends a little way onto the distal scapus where it fades out. The distal part of the scapulus is translucent and bluish-grey, and the actinopharynx, which is pinkish-brown, is clearly visible through it. There are eight prominent chalk-white blotches, longitudinally elongated and each corresponding with a macrocoel, which occur on the chestnut coloured region just above the distal edge of the periderm (fig. 2a).

The scapulus narrows slightly towards the rather indistinct capitulum which bears a narrow semi-opaque white streak in the middle of each macrocoel, each about half the length of the white markings on the scapulus (fig. 2a).

Disc. The disc is circular, its diameter less than that of the scapulus. It bears a prominent hypostome which, together with the tapering scapulus, approximates to the shape of a truncated cone in living anemones (fig. 2a). The colour of the disc varied from opaque deep chestnut brown to almost colourless and translucent. The hypostome was always off-white and the macrocneme insertions were frequently marked with continuations of the hypostome pigment, extending over the margin just onto the capitulum.

Tentacles. Typically, the tentacles numbered 16 in two cycles of 8, presumably the normal adult pattern. The endocoelic (inner) tentacles were longer than the exocoelic (outer) tentacles. All the tentacles were colourless and translucent except for a more or less strongly marked white tip. Table 1 shows the numbers of tentacles counted on 25 specimens (16 from fixed samples and 9 living). The range was from 12 to 18 with a mode of 16 (80% of the specimens). Only one specimen had supernumerary tentacles. The tentacles were delicate in form and, in living specimens of about 2.5 mm diameter scapus, they tapered from just over 0.4 mm in diameter at the base to a fine point: inner tentacles about 11.25 mm long, outer tentacles about 9 mm long. In unburied specimens the tentacles tended to be blunter and shorter by about one half. In the fixed specimens, the tentacles were either completely withdrawn or contracted to 1 mm or less.

**TABLE 1: Numbers of tentacles counted on 25 specimens of** *E. meridionalis*

| Number of tentacles | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|
| Number of specimens | 1 | 0 | 1 | 2 | 20 | 0 | 1 |
| Percentage of specimens | 4 | 0 | 4 | 8 | 80 | 0 | 4 |

Anatomy. The description is based on dissections of nine whole fixed specimens and two living specimens, and examinations of two series of transverse sections and one series of longitudinal sections. The arrangement of the tentacles and mesenteries of *E. meridionalis* presents nothing unexpected, the two cycles of eight tentacles being associated with eight microcnemes (present only at the level of the capitulum) and eight macrocnemes. This is typical of an *Edwardsia* species with sixteen tentacles (see fig. 1a; Stephenson, 1935, fig. 45B; Carlgren, 1949, plate I, fig. 1). The fact that the inner tentacles are longer than the outer is, however, rather unusual.

The retractor muscles, at all levels of the column (figs. 4 to 7), had in cross-section a branched process (rarely two) in the outer part and between two and six other less branched or single processes in the inner part. The parietal muscles, however, varied in cross section depending on the level in the column. In the distal column, they were hastate in cross-section (figs. 4 and 5), becoming foliiform with six to ten processes more proximally (figs. 6 and 7). The extension of the parietal muscles onto the distal column wall was slight. However, towards the proximal end of the column, it became progressively more marked, though nowhere greatly exceeding the maximum width of the foliiform portion (figs. 4 to 7). Circular muscle was attached to the inner surface of the mesogloea at the base of the endoderm (figs. 4 to 8). The cnidoglandular tracts of the mesenterial filaments possessed many secretory cells containing granules about 1$\mu$m in diameter.

The mesogloea, at least in fixed and contracted specimens, was thinnest at the extreme distal and proximal ends of the column. At the distal end, it bore short radial

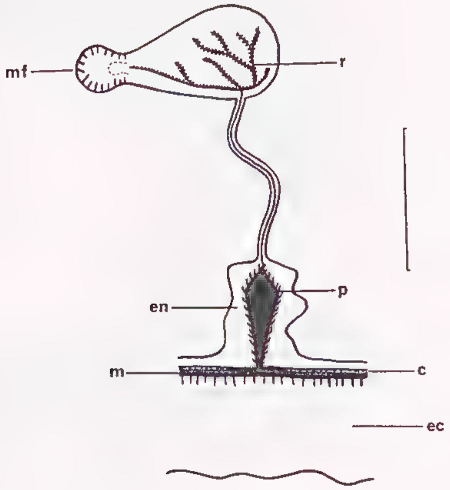

Figure 4. — Transverse section of macrocneme and part of body wall at the level of the scapulus of *E. meridionalis*, 0.9 mm in diameter; scale = 100 μm.
c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea; mf = mesenterial filament; p = parietal muscle; r = retractor muscle.

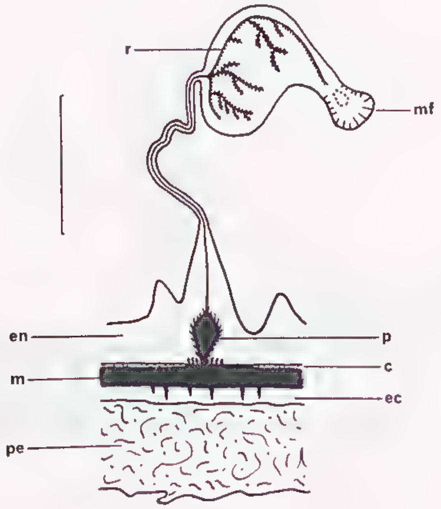

Figure 5. — Transverse section of macrocneme and part of body wall at the level of the upper scapus of *E. meridionalis*, 0.9 mm in diameter; scale = 100 μm.
c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea; mf = mesenterial filament; p = parietal muscle; pe = periderm; r = retractor muscle.

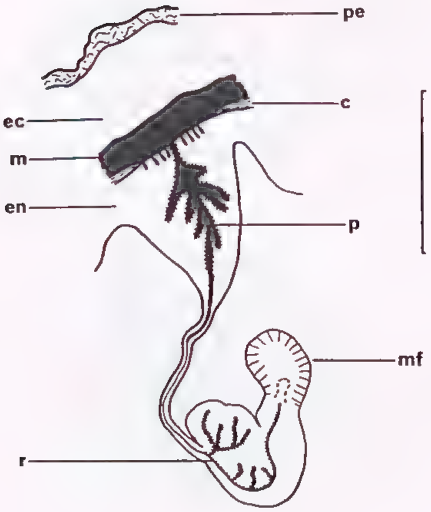

Figure 6. — Transverse section of macrocneme and part of body wall at the level of the middle scapus of *E. meridionalis,* 0.9 mm in diameter; scale = 100$\mu$m.
c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea; mf = mesenterial filament; p = parietal muscle; pe = periderm; r = retractor muscle.

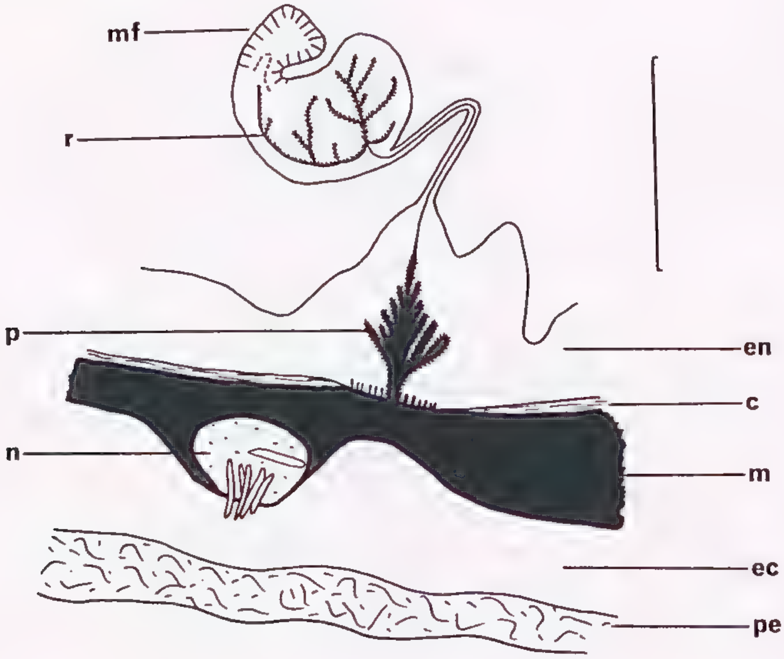

Figure 7. — Transverse section of macrocneme and part of body wall at the level of the lower scapus of *E. meridionalis,* 0.9 mm in diameter; scale = 100$\mu$m.
c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea; mf = mesenterial filament; n = nemathybome; p = parietal muscle; pe = periderm; r = retractor muscle.

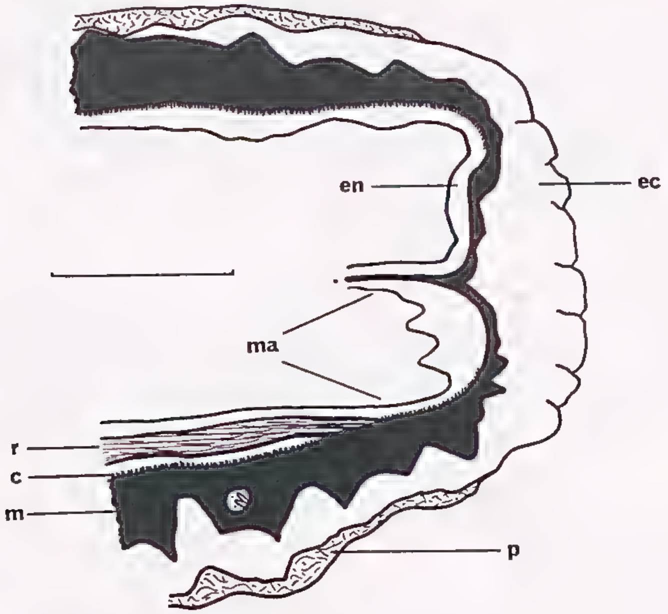

Figure 8. — Longitudinal section of physa and lower scapus of *E. meridionalis*, 1 mm in diameter; scale = 100 μm.
c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea containing a nemathybome; ma = macrocnemes; p = periderm; r = retractor muscle.

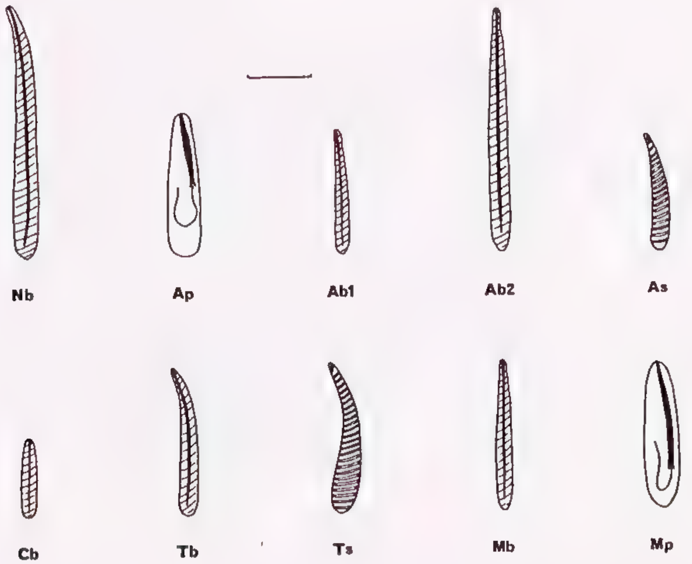

Figure 9. — Stylized representation of the cnidom of *E. meridionalis;* scale = 10 μm.
Nb = microbasic *b*-mastigophore of nemathybome.
Ap = microbasic *p*-mastigophore of actinopharynx; Ab1 and Ab2 = microbasic *b*-mastigophores of actinopharynx; As = spirocyst of actinopharynx.
Cb = microbasic *b*-mastigophore (?) of column.
Tb = microbasic *p*-mastigophore of tentacle; Ts = spirocyst of tentacle.
Mb = microbasic *p*-mastigophore of mesenterial filament; Mp = microbasic *p*-mastigophore of mesenterial filament.

processes projecting into the ectoderm (figs. 4 and 5): such processes did not occur anywhere else. In addition, there were thickenings of the mesogloea in the form of longitudinal ridges extending into the ectoderm opposite each macrocoel which gave a polygonal appearance to the scapulus in fixed specimens. The nemathybomes were embedded in the scapus mesogloea (possibly not extending to the most distal part) and contained from about seven to at least fifteen nematocysts of one type (microbasic *b*-mastigophores) and numerous granules up to about 2.1$\mu$m in diameter. In a transverse section, usually only one nemathybome was cut through in each macrocoel but occasionally two were seen.

The periderm plus the closely associated foreign material (including sand, detritus and diatoms) was up to 65$\mu$m thick (the periderm alone being about 2.6$\mu$m thick) in contracted specimens. The periderm must be much thinner when stretched as in fig. 2b. The imperforate physa was morphologically differentiated from the scapus by its lack of circular muscle, of periderm and of nemathybomes, and by its thick ectoderm and thin mesogloea (fig. 8).

The sexes are probably separate (data from fixed specimens collected in December, during the Antarctic summer). The sperm heads were pointed as is usual in *Edwardsia* species (see Schmidt, 1974), about 3.1$\mu$m long and 2.1$\mu$m wide. The oocytes were spherical or elliptical in shape: the smallest measured was 22.8$\mu$m in diameter (nucleus 10.3$\mu$m diameter, nucleolus 5.2$\mu$m diameter) and the largest was 147.9$\mu$m in diameter (nucleus 31.0$\mu$m diameter, nucleolus 13.4$\mu$m diameter).

Cnidom. The description is based on examinations of four living specimens, twelve fixed specimens (including the holotype and both paratypes) and series of transverse sections of two further specimens. Up to fourteen cnidae of each type were measured from each tissue sample. The cnidom is summarized in table 2 and the types of cnidae are shown in stylized form in fig. 9. Besides those in the nemathybomes, nematocysts in the column wall are probably very rare: only two were found in seven tissue samples. Examination of stained transverse sections confirmed their rarity but it was still not possible to be absolutely certain of their type since no discharged examples were seen. They are shown as microbasic *b*-mastigophores, but may be basitrichs, these types being difficult to distinguish when undischarged (see Carlgren, 1940 and p.329). The larger microbasic *b*-mastigophores in the actinopharynx were found in only two out of five tissue samples; they are unlikely to have been contaminants since the nematocysts closest in appearance to them occur in the nemathybomes and furthermore the latter type is usually slightly curved whilst that in the actinopharynx is usually straight (see fig. 9). However, the spirocysts found in two out of five actinopharynx samples might possibly be contaminants from the tentacles or disc, although Carlgren (1940) noted the presence of spirocysts in the actinopharynges of some other Actiniaria. The microbasic *p*-mastigophores in the mesenterial filaments were found in only two out of four tissue samples and were rare in these; they appear to be similar to those in the actinopharynx. Microbasic *b*-mastigophores were found in the mesenterial filaments, which confirms the presence of this type of nematocyst in *Edwardsia* filaments noted for the first time by Manuel (1977).

Variation. The appearance of the living specimens examined was fairly constant: figs. 2a and b show typical specimens. Only two variants were observed which, although similar in form to the other specimens, bore only white pigment. This occurred at the tips of the tentacles, on the hypostome and in the form of eight blotches just above the junction of scapus and scapulus, all as described for normal specimens. However, the actinopharynx was also white but other parts of these specimens were devoid of pigment, being translucent.

**TABLE 2: The cnidom of *E. meridionalis* (measurements in $\mu$m)**

| Tissues | Cnidae | Mean sizes | Ranges | Abundance |
|---|---|---|---|---|
| Tentacle tips | Spirocysts | 23.4 x 4.1 | 10.3-39.3 x 2.1-5.2 | Common |
| | Microbasic *b*-mastigophores | 22.5 x 2.7 | 20.7-26.9 x 2.1-3.6 | Common |
| Column | Microbasic *b*-mastigophores (?) | 12.4 x 2.1 | 10.3-15.5 x 2.1 | Very rare |
| Nemathybomes | Microbasic *b*-mastigophores | 39.0 x 3.6 | 29.0-50.7 x 2.6-4.7 | See p.336 |
| Actinopharynx | Microbasic *b*-mastigophores | 19.3 x 1.9 | 14.5-23.8 x 1.6-2.6 | Predominant |
| | Microbasic *p*-mastigophores | 22.1 x 4.9 | 14.5-25.9 x 3.6-5.7 | Few |
| | Microbasic *b*-mastigophores | 37.6 x 3.1 | 35.7-40.3 x 2.6-4.1 | Rare |
| | Spirocysts | 17.6 x 2.6 | 14.5-22.8 x 2.1-3.1 | Very rare |
| Mesenterial filaments | Microbasic *b*-mastigophores | 23.1 x 2.2 | 18.6-25.9 x 1.6-3.1 | Predominant |
| | Microbasic *p*-mastigophores | 22.8 x 5.0 | 20.7-25.9 x 3.6-6.2 | Rare |

## ECOLOGY: HABITAT OF *E. MERIDIONALIS*

The information in this part was provided by Dr J. K. Lowry and Mr J. S. Oliver.

In McMurdo Sound *E. meridionalis* inhabits a zone between 30 and 180 m in depth along the western Cape Bird coastline at the northern end of Ross Island; and between 5 and 40 m in depth at Cape Armitage at the southern end of Ross Island and also on the western side of the Sound. Population densities at various depths are shown in table 3.

**TABLE 3: Numbers per m² of *E. meridionalis* at various depths (Antarctic summer samples)***

| Depth (m) | Ross Sea | Marble Point | New Harbour | Ferrar Glacier | McMurdo Station Jetty | Cape Armitage | Cape Bird |
|---|---|---|---|---|---|---|---|
| 6 | — | — | — | — | — | 2,744 | — |
| 7 | — | — | 224 | — | — | — | — |
| 9 | — | — | — | — | — | 7,560 | — |
| 10 | — | — | 7,560 | — | — | — | — |
| 18 | — | — | — | — | — | 560 | — |
| 20 | — | — | 12,700 | — | 19,000 | — | — |
| 25 | — | — | 1,230 | — | — | 500 | — |
| 30 | — | 2,770 | — | 0-50 | — | — | — |
| 35 | — | — | — | — | — | — | 23,500 |
| 50 | — | — | — | — | — | — | 19,250 |
| 65 | | — | — | — | — | — | 10,800 |
| 500 | 0-3 | — | — | — | — | — | — |

* Data provided by Mr J. S. Oliver and Dr J. K. Lowry
— No data

At Cape Bird between 30 and 50 m depth the substrate is medium to very fine sand with a mean particle diameter of 170 μm. *E. meridionalis* lives here in a community dominated by the tube building spionid polychaete *Spiophanes tcherniai* Fauvel; these two species along with the myodocopid ostracod *Philomedes heptathrix* Kornicker and the tanaidacean *Nototanais dimorphus* Beddard make up about 77% numerically of the total animal population. At Cape Armitage *E. meridionalis* lives in mud, sand, gravel, sponge spicule and cobble substrates, comprizing zones, I, II and III of Dayton, Robilliard and Paine (1970); the gravel with which the living anemones used in this study were received came from a depth of 10 m and analysis by sieving showed it to have a mean particle diameter of 540 μm. In shallow water, *Edwardsia* is most abundant just above the level of the dense maldanid and spionid polychaete tubes; these tubes cannot be maintained towards extreme shallows because they probably provide a substrate for ice crystal formation. *Edwardsia* does not have this problem and flourishes just above the tube zone and below the zone of permafrost or the anchor ice carpet. On the other side of McMurdo Sound at New Harbour, the tube zone is not present and *Edwardsia* is more abundant somewhat deeper in the shallows. Benthic diatom growth or the grazing activities of asteroids and ophiuroids may control the lower limit of this dense zone at New Harbour (*i.e.* in depths greater than *ca* 20 m). *E. meridionalis* is the un-named *Edwardsia* species included by Dayton and Oliver (1977) amongst "other Vermes" in the Antarctic benthic samples in their table 1.

Littlepage (1965) has summarized the physical conditions in southern McMurdo Sound at depths from 3 to 275 m: the annual mean temperature is −1.87°C (range −2.15 to −1.40°C); the annual mean salinity is 34.70‰ (range 33.96 to 34.99‰).

## GEOGRAPHICAL DISTRIBUTION OF *E. MERIDIONALIS*

*E. meridionalis* has been found at several localities in McMurdo Sound, *viz.* Cape Bird, Ross Island (77°13′S, 166°25′E); Cape Armitage, Ross Island (77°51′S, 166°41′E); McMurdo Station Jetty (77°54′S, 166°38′E); Ferrar Glacier (77°42′S, 163°36′E); New Harbour (77°34′S, 163°34′E); Marble Point (77°25′S, 163°47′E) and also in the open Ross Sea (74°58′S, 170°48′E). (These co-ordinates are approximate and were estimated from maps.) In McMurdo Sound, it appears to be most abundant at depths from 6 to 65 m and is much less frequent at 500 m in the Ross Sea (table 3).

As noted previously, it is possible that some of the specimens assigned to *E. intermedia* by Carlgren (1899, 1927a, 1959) may belong to *E. meridionalis*. If this is so, then the distribution may include Graham Land, South Georgia, Tierra del Fuego and Southern Chile, all these records being from depths within the range recorded for *E. meridionalis* from McMurdo Sound and the Ross Sea. Records of *E. meridionalis* and of specimens identified as *E. intermedia* by Carlgren (1899, 1927a, 1959) are shown in fig. 10.

## DIFFERENTIATION OF *E. MERIDIONALIS* SP. NOV. FROM OTHER NOMINAL *EDWARDSIA* SPECIES

The most useful diagnostic features of *Edwardsia* species are the types and sizes of the nematocysts in the nemathybomes; the arrangement and prominence of the nemathybomes on the scapus; the types and sizes of the nematocysts in the actinopharynx; the arrangement of the mesenteries and tentacles in adult specimens; and in some species, the branching patterns seen in transverse sections of retractor and parietal muscles. The appearance of the nemathybome arrangement and, maybe to a lesser extent, that of the retractor muscles may be affected by the degree of contraction of an anemone and severe distortion may occur in preserved specimens. Transverse sections of longitudinal muscles also may vary in appearance depending on the level of the section through the column. Other anatomical features and patterns of coloration may under some circumstances serve to identify incompletely described specimens, but only when especially distinctive and known to be consistent.

An attempt has been made to trace all the published descriptions of nominal *Edwardsia* species. Each has been compared with the foregoing description of *E. meridionalis*. Discounting the invalid species listed in appendix III, 39 *nomina clara* (*sensu* Smith, 1963) remain. These may be differentiated from *E. meridionalis* by a process of elimination using various combinations of the diagnostic features noted above. For the sake of brevity, only some of the distinctive features are given here: further details may be obtained from the references given.

(1) First, those *Edwardsia* species with two nematocyst types in the nemathybomes and (with the exception of *E. delapiae*) having a different arrangement of nemathybomes from that of *E. meridionalis* are excluded as follows:—

*E. beautempsii* de Quatrefages, 1842. Nemathybomes in eight longitudinal lines (Manuel, 1977).

*E. timida* de Quatrefages, 1842. Nemathybomes scattered (Manuel, 1977).

*E. tuberculata* Düben and Koren, 1847. Tuberculate nemathybomes in eight longitudinal lines (Carlgren, 1921).

*E. sipunculoides* (Stimpson, 1853). Nemathybomes scattered (Carlgren, 1931).

*E. sulcata* Verrill, 1866. Nemathybomes possibly in eight longitudinal lines, but at any rate not scattered (Carlgren, 1950a).

*E. claparedii* (Panceri, 1869). Tuberculate nemathybomes in eight longitudinal lines (Carlgren and Stephenson, 1928 as *E. callimorpha* (Gosse) ).

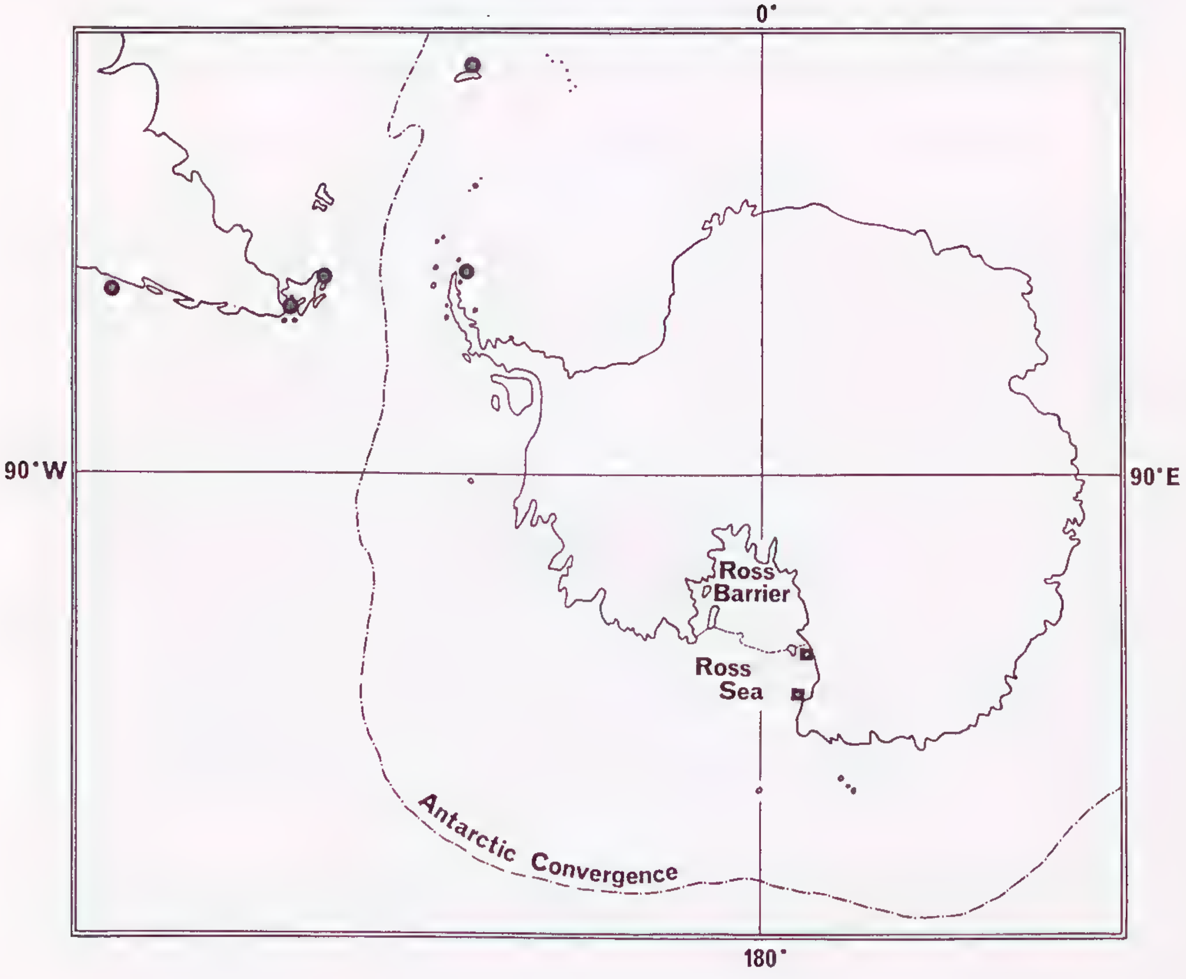

Figure 10. — Geographical distribution of *E. meridionalis* (▣) and specimens identified by Carlgren as *E. intermedia* (◉), some of which may be conspecific with *E. meridionalis*. The *E. meridionalis* symbol in McMurdo Sound represents 6 separate localities (see p.339). The *E. intermedia* symbol off Chile represents 8 separate localities (see Carlgren, 1959).

*E. elegans* Verrill, 1869. NematHybomes in eight longitudinal lines (Carlgren, 1931).

*E. neozelanica* Farquhar, 1898. Nemathybomes scattered giving granulous appearance (Carlgren, 1924 as *E. tricolor* Stuckey).

*E. californica* (McMurrich, 1913). Nemathybomes in eight longitudinal lines (Carlgren, 1936).

*E. tinctrix* Annandale, 1915. Tuberculate nemathybomes in eight longitudinal lines (Annandale, 1915; Carlgren, 1925).

*E. danica* Carlgren, 1921. Nemathybomes more or less scattered (Carlgren, 1921).

*E. longicornis* Carlgren, 1921. Tuberculate nemathybomes in eight longitudinal lines, physa perforate (Carlgren, 1921).

*E. delapiae* Carlgren and Stephenson, 1928. Nemathybomes in a wide band in the centre of each macrocoel (Carlgren and Stephenson, 1928).

*E. maroccana* Carlgren, 1931. Nemathybomes in eight longitudinal lines (Carlgren, 1931).

*E. octoradiata* Carlgren, 1931. Nemathybomes in eight longitudinal lines (Carlgren, 1931).

*E. capensis* Carlgren, 1938. Nemathybomes in eight longitudinal lines (Carlgren, 1938).

*E. sanctaehelenae* Carlgren, 1941. Nemathybomes in eight longitudinal lines (Carlgren, 1941).

*E. annamensis* Carlgren, 1943. Nemathybomes in eight longitudinal lines (Carlgren, 1943).

*E. ivelli* Manuel, 1975. Tuberculate nemathybomes in eight longitudinal lines (Manuel, 1975).

*E. carlgreni* nom. nov. Nemathybomes in closely packed groups (Carlgren, 1921 as *E. pallida* Carlgren).

(2) Second, those species with only one type of nematocyst (of a size range not or only slightly overlapping that in *E. meridionalis*) in the nemathybomes (which, with the exception of *E. andresi*, are differently arranged) are excluded as follows:—

*E. andresi* Danielssen, 1890. Nemathybomes (nematocysts 48-67 x 3.5-4 μm) irregularly arranged but concentrated in the centres of the macrocoels, physa perforate (Carlgren, 1921).

*E. vegae* Carlgren, 1921. Nemathybomes (nematocysts 84-101 x 3μm) visible to the naked eye and scattered, physa perforate (Carlgren, 1921).

*E. kameruniensis* Carlgren, 1927b. Nemathybomes (nematocysts 45-63 x 3.5-4.5μm) scattered (Carlgren, 1927b).

*E. armata* Carlgren, 1931. Nemathybomes (nematocysts 43-70 x 3.5-4.5μm) scattered (Carlgren, 1931).

*E. japonica* Carlgren, 1931. Nemathybomes (nematocysts 74-101 x 2.5-3.5 μm) scattered (Carlgren, 1931).

*E. norvegica* Carlgren, 1942. Nemathybomes (nematocysts 47-58 x 3μm) scattered (Carlgren, 1942).

*E. jonesii* Seshaiya and Cuttress, 1969. Nemathybomes (nematocysts 48-72 x 4.5-5.5 μm) in eight longitudinal lines (tending to become sixteen lines around mid-scapus) (Seshaiya and Cuttress, 1969).

(3) Third, those species with types and sizes of nematocysts in the actinopharynx differing from those in *E. meridionalis* (and having other significant differences) are excluded as follows:—

*E. pudica* Klunzinger, 1877. Retractor muscles extremely diffuse (Faurot, 1895 as *E. adenensis* Faurot; Carlgren, 1931).

*E. fusca* Danielssen, 1890. Distinctive coloration different from that of *E. meridionalis* (cf. Carlgren, 1921).

*E. vitrea* (Danielssen, 1890). Nemathybomes scattered, physa perforate (Carlgren, 1921).

*E. arctica* Carlgren, 1921. Tuberculate nemathybomes in eight longitudinal lines, physa perforate (Carlgren, 1921).

*E. finmarchica* Carlgren, 1921. Nemathybomes scattered, physa perforate (Carlgren, 1921).

*E. islandica* Carlgren, 1921. Nemathybomes scattered (Carlgren, 1921).

*E. bocki* Carlgren, 1931. Nemathybomes scattered (Carlgren, 1931).

*E. duodecimtentaculata* Carlgren, 1931. Maximum of twelve tentacles (Carlgren, 1931).

*E. stephensoni* Carlgren, 1950b. Nemathybomes scattered (Carlgren, 1950b).

(4) Last, those species not falling into the first three groups, but having other distinctive characters, are excluded as follows:—

*E. carneola* (Verrill, 1928). Has twenty-four tentacles and a distinctive coloration different from that of *E. meridionalis* (*cf.* Verrill, 1928 as *Edwardsiella carneola* Verrill).

*E. gilbertensis* Carlgren, 1931. Nemathybomes in eight longitudinal lines (Carlgren, 1931).

*E. vivipara* Carlgren, 1950c. Nemathybomes scattered, twelve tentacles and diffuse retractors (Carlgren, 1950c).

## THE STATUS OF ANEMONES DETERMINED AS *E. INTERMEDIA* McMURRICH, 1893

The name *E. intermedia* McMurrich, 1893 is here regarded as a *nomen dubium* (see p. 349). The holotype was sectioned and I do not know its whereabouts, if indeed it still exists. However, Carlgren (1899, 1927a, 1959) has determined several anemones from Subantarctic regions and South American waters as this species. Since some, at least, of these specimens have features in common with *E. meridionalis*, their status is discussed in detail. Although the single type-specimen of *E. intermedia* was incompletely described, the fact that its nemathybomes were scattered and visible to the naked eye immediately differentiates it from *E. meridionalis,* but not from some other *Edwardsia* species.

The anemones from the Magellan Strait (Chile), Ushuaia (Tierra del Fuego) and South Georgia determined by Carlgren (1899) as *E. intermedia* may belong to two or more species. They were described as having scattered nemathybomes. Later (Carlgren, 1927a), some of the same specimens were re-examined and the measurements of the nematocysts in their nemathybomes were given. Similar but more extensive data were also given for further anemones from South Georgia and Graham Land (Carlgren, 1927a) and they appear to be similar to those of *E. meridionalis* from McMurdo Sound (table 4). Further details of the cnidom of specimens from Chile (Carlgren, 1959) are also included in table 4.

Compared with the McMurdo Sound populations of *E. meridionalis,* Carlgren's specimens show great variation in numbers of tentacles on each individual (Carlgren, 1899, 1927a, 1959). In the case of an edwardsiid with a finite number of tentacles in the adult state, one would expect a population to have most individuals with tentacles up to and including this number, as in, for example, *Nematostella vectensis* Stephenson, 1935 (see Williams, 1975). This appears to be true of *E. meridionalis* since only one specimen examined had supernumerary tentacles, the adult number apparently being 16 (table 1). However, Carlgren's specimens have from 16 to 28 tentacles; so it is extremely unlikely that the adult number can be 16 if they are all the same species. It is remarkable, moreover, that with the great variation in the numbers of tentacles and also in the appearance of transverse sections of the retractor muscles (see figs. 2 and 3 of Carlgren

**TABLE 4: A comparison of the size ranges(μm) of cnidae in *E. meridionalis* and *E. intermedia* (*sensu* Carlgren)**

| | *E. meridionalis* | *E. intermedia* | | |
|---|---|---|---|---|
| | present study: McMurdo Sound | Carlgren (1927a): Magellan Strait, Ushuaia, South Georgia | Carlgren (1927a): South Georgia, Graham Land | Carlgren (1959): Chile |
| Tentacles | 10.3-39.3 x 2.1-5.2 (sp.) | — | 14-24 x 1.5-3.5 (sp.) | — |
| | 20.7-26.9 x 2.1-3.6 (m. *b*-m.) | — | 21-26 x 2-2.5(?) | 15-36 x 2.5-3 (bas.) |
| Column | 10.3-15.5 x 2.1 (m. *b*-m.) | — | 15-19 x 2.5 (?) | — |
| Nemathybomes | 29.0-50.7 x 2.6-4.7 (m. *b*-m.) | 35-53 x 3-4 (?) | 34-53 x 3-4 (?) | 29.6-63.4 x 3-4 (?) |
| Actinopharynx | 14.5-23.8 x 1.6-2.6 (m. *b*-m.) | — | — | — |
| | 14.5-25.9 x 3.6-5.7 (m. *p*-m.) | — | 24-26 x 5 (?) | — |
| | 35.7-40.3 x 2.6-4.1 (m. *b*-m.) | — | 31-41 x 3-4 (?) | 31-52 x 4.2-5.6 (bas.) |
| | 14.5-22.8 x 2.1-3.1. (sp.) | — | — | — |
| Mesenterial filaments | 18.6-25.9 x 1.6-3.1 (m. *b*-m.) | — | — | 21-24 x 2.8 (bas.) |
| | 20.7-25.9 x 3.6-6.2 (m. *p*-m) | — | — | 24-35 x 5.6-6.3 (m. *p*-m.) |
| | — | — | — | 31-49 x 4.2-5.6 (bas.) |

sp. = spirocysts
m. *b*-m. = microbasic *b*-mastigophores
m. *p*-m. = microbasic *p*-mastigophores
bas. = basitrichs
? = nematocyst type not stated
— = nematocysts not recorded

(1927a) and fig. 1 of Carlgren (1959) ) there should be such similarity between the sizes of nematocysts in the nemathybomes and other tissues of his specimens. However, the nemathybomes have variable distributions (see Carlgren, 1899, 1959) and it is noteworthy that the retractor and parietal muscles described by Carlgren (1927a, 1959) are quite different from those of *E. meridionalis.*

It is concluded that in view of the poor description of the single specimen of *E. intermedia,* Carlgren could hardly have identified his material with this nominal species with any certainty. On the other hand, despite a similarity between the nemathybome and other nematocysts of some of his specimens and those of *E. meridionalis,* there seems to be too much variation in his subsequent descriptions to be sure of the conspecificity of all of his specimens with the latter species. Indeed, the present confusion regarding *E. intermedia* is perhaps best summarized by Carlgren himself (1959): "The identification of the individuals here mentioned is rather uncertain as the single type specimen is imperfectly described . . . I identified (1927a) some individuals from Tierra del Fuego, South Georgia and Graham Land with *intermedia*. They may not be referable to this species because the nematocysts of the nemethybomes are shorter than in our specimens, but the number of tentacles is greater."

## DISCUSSION

The genus-group name *Edwardsia* de Quatrefages, 1841, currently used for the genus of actiniarians dealt with in this paper, is preoccupied by *Edwardsia* O. G. Costa, 1834 (Crustacea): this homonymy invalidates the family-group name Edwardsiidae Andres, 1881. A request (Williams, 1979) has been made to the International Commission on Zoological Nomenclature for suppression of the name *Edwardsia* O. G. Costa and conservation of the names *Edwardsia* de Quatrefages and Edwardsiidae Andres. A brief outline of this request appears in appendix I.

The species *E. meridionalis* sp. nov. now described does not fit the generic definition of *Edwardsia* by Carlgren (1949), by virtue of its having the inner tentacles longer than the outer. Stephenson (1935, p.34) had already suggested that it may be advisable to place any species of edwardsiid possessing nemathybomes and having inner tentacles longer than the outer in a new genus. The only major difference between Carlgren's (1949) generic definition and that of Manuel (1977) is the omission by the latter author of any reference to the relative lengths of inner and outer tentacles. However, the present description of *E. meridionalis* and the description of *E. sipunculoides* by Verrill (1866), both with inner tentacles longer than the outer, provide justification for Manuel's (1977) amendment of Carlgren's (1949) generic definition. This makes unnecessary the proposal of a new genus to accommodate edwardsiid species with the inner tentacles longer than the outer and possessing nemethybomes, as suggested by Stephenson (1935).

Carlgren (1921) suggested that all members of the genus *Edwardsia* might have a perforate physa, although he did not include this feature in his generic definition. It is now known, however, that some *Edwardsia* species (*e.g., E. beautempsii* (see Manuel, 1977) and *E. meridionalis*) do have an imperforate physa.

It is interesting that anemones of the genus *Edwardsia* have been found so infrequently in Antarctic and Subantarctic seas. None was identified by Carlgren (1903, 1914, 1928, 1930, 1939), Carlgren and Stephenson (1929), Clubb (1902, 1908), Grebelny (1975), Mann (1948), Pax (1922, 1924a, 1926), Roule (1909) or Stephenson (1918), although some of the anemones examined by these authors were collected from McMurdo Sound where *E. meridionalis* is to be found. In some instances at least, the collecting gear used probably took only larger species: for instance, the sizes of the preserved specimens of trawled anemones recorded by Stephenson (1918), which would have been even larger in life, are all much greater than the size of living specimens of *E. meridionalis*. Specimens assigned to *E. intermedia* by Carlgren (1899, 1927a, 1959) have already been discussed; the distribution of *E. meridionalis* will possibly become clearer when the true identity of Carlgren's material is determined. Carlgren's (1928) discussion of the distribution of *E. intermedia* may then have to be reconsidered.

Appendix II comprises a list of the names of all presently accepted *Edwardsia* species with notes on their synonyms and their geographical distributions. Appendix III is a list of nominal *Edwardsia* species here regarded as invalid.

## ACKNOWLEDGEMENTS

I am grateful to Dr J. K. Lowry for providing me with fixed specimens of *E. meridionalis* and to Mr J. S. Oliver for diving for the living specimens. My thanks are also due to Dr P. F. S. Cornelius, Mr R. L. Manuel, Dr Lowry and Mr Oliver for valuable comments on the manuscript. Mr Manuel kindly took the photographs and prepared the sections. I am grateful also to Mrs S. C. Williams for undertaking the typing of the manuscript.

## APPENDIX I

### THE USAGE OF THE NAME *EDWARDSIA* DE QUATREFAGES, 1841

The problems relating to the homonymy between the generic names *Edwardsia* O. G. Costa, 1834 and *Edwardsia* de Quatrefages, 1841 can be summarized as follows.

The genus-group name *Edwardsia* has been proposed in five separate publications for different taxa, and replacement names have been proposed for the four junior homonyms (see Neave, 1939). The senior homonym, *Edwardsia* O. G. Costa, 1834 was long ago synonymized with *Sapphirina* Thompson, 1829, applied to a poecilostomatoid copepod (*e.g.* Giesbrecht, 1892). However, the oldest junior homonym, *Edwardsia* de Quatrefages, 1841, has been used regularly up to the present time and, furthermore, it is the name of the type-genus of the family Edwardsiidae Andres, 1881. The replacement name once proposed for *Edwardsia* de Quatrefages is *Milnea* Reichenbach *in* Wright, 1866 but it has apparently not been used since Wright's paper appeared and is regarded as an unavailable name (Williams, 1979).

Thus the little-used and now synonymized *Edwardsia* O. G. Costa threatens the established usage of *Edwardsia* de Quatrefages. Confusion would be caused by the use of a replacement name for *Edwardsia* de Quatrefages since the widely used actinian genus-group name *Edwardsia* would fall out of use. The family-group name Edwardsiidae Andres, 1881 is invalid since the name of its nominal type-genus, *Edwardsia* de Quatrefages, 1841, is a junior homonym. A request (Williams, 1979) has therefore been made to the International Commission on Zoological Nomenclature for suppression of the genus-group name *Edwardsia* O. G. Costa, 1834 and conservation of *Edwardsia* de Quatrefages, 1841 and also of the family-group name Edwardsiidae Andres, 1881.

The solution to these problems is dependent upon the publication of an Opinion by the Commission, and in the meantime the accepted usages of the names *Edwardsia* de Quatrefages and Edwardsiidae Andres have been followed in this paper.

## APPENDIX II

## CURRENTLY ACCEPTED *EDWARDSIA* SPECIES, THEIR SYNONYMS AND DISTRIBUTIONS

Of the nominal species of *Edwardsia* which were found in the literature, many are at present considered to be invalid (see appendix III). The remaining *nomina clara* (*sensu* Smith, 1963) are listed below with *E. meridionalis* sp. nov. The question of whether some of these *nomina clara* are valid names or not can probably only be decided after examination of type material, if available, or live specimens but is beyond the scope of the present paper.

*Edwardsia beautempsii* de Quatrefages, 1842. This is the type species by subsequent designation (Carlgren, 1949), since no nominal species were included at the time the genus was established. Distribution: northern France.

*E. timida* de Quatrefages, 1842. Junior subjective synonyms: *E. harassi* de Quatrefages, 1842 (*q.v.*); *Edwardsiella harassii* — Andres (1883); ?*Fagesia* (≡ *Milneedwardsia*) *dixonii* (Carlgren, 1921) (see Manuel, 1977); *E. callianthus* Rawlinson, 1935 (*q.v.*); *non E. timida* (*sensu* Walton and Rees, 1913) (see Stephenson, 1935). Junior objective synonym: *Edwardsiella timida* — Andres (1883). Distribution: northern France, north Wales, eastern Ireland.

*E. tuberculata* Düben and Koren, 1847. Distribution: western Scandinavia (Denmark, Sweden, Norway) and southern Iceland.

*E. sipunculoides* (Stimpson, 1853). Synonyms: *Actinia sipunculoides* Stimpson, 1853; *Edwardsiella sipunculoides* — Andres (1883). Distribution: Alaska and N.E. North America.

*E. sulcata* Verrill, 1866. Distribution: eastern United States.

*E. claparedii* (Panceri, 1869). Synonyms: *Halcampa claparedii* Panceri, 1869; *E. timida* (*sensu* Walton and Rees, 1913) (see Stephenson, 1935); *E. callimorpha* (*sensu* Stephenson, 1935); *non E.* (*Scolanthus*) *callimorpha* (Gosse, 1853) (see Manuel, in preparation). Distribution: southern Italy, northern France, southern and western England, southern Ireland.

*E. elegans* Verrill, 1869. Distribution: N.E. North America.

*E. pudica* Klunzinger, 1877. Junior subjective synonym: *E. adenensis* Faurot, 1895 (*q.v.*). Junior objective synonym: *Edwardsiella pudica* — Andres (1883). Distribution: Zanzibar, Gulf of Aden, Red Sea, southern India.

*E. andresi* Danielssen, 1890. Distribution: Denmark, Norway to Spitzbergen, Iceland, western Greenland.

*E. fusca* Danielssen, 1890. Distribution: southern Barents Sea.

*E. vitrea* (Danielssen, 1890). Synonym: *Edwardsioides vitrea* Danielssen, 1890. Distribution: eastern Greenland, Spitzbergen.

*E. neozelanica* Farquhar, 1898. Synonyms: *E. elegans* Farquhar, 1898 (≡*E. tricolor* Stuckey, 1909) (*q.v.*). Distribution: New Zealand.

*E. californica* (McMurrich, 1913). Synonym: *Edwardsiella californica* McMurrich, 1913. Distribution: south-western United States.

*E. tinctrix* Annandale, 1915. Distribution: north-eastern and western India.

*E. arctica* Carlgren, 1921. Distribution: Arctic (eastern Greenland to Kara Sea) and Sea of Japan (?).

*E. danica* Carlgren, 1921. Distribution: Baltic Sea, Denmark, Heligoland.

*E. finmarchica* Carlgren, 1921. Distribution: northern Norway.

*E. islandica* Carlgren, 1921. Distribution: Iceland.

*E. longicornis* Carlgren, 1921. The cnidom and certain other features of this species and *E. beautempsii* de Quatrefages, 1842 are very similar and the two species may prove to be identical (see Manuel, 1977). Distribution: Denmark.

*E. vegae* Carlgren, 1921. Distribution: Arctic Sea of Siberia.

*E. kameruniensis* Carlgren, 1927b. Distribution: Cameroun.

*E. carneola* (Verrill, 1928). Synonym: *Edwardsiella carneola* Verrill, 1928. Distribution: Kauai (Hawaii).

*E. delapiae* Carlgren and Stephenson, 1928. Although this species was accepted as valid by Manuel (1975), he later considered that it was in part synonymous with *E. timida* de Quatrefages, 1842 (see Manuel, 1977). Certain aspects of the cnidom, anatomy and coloration agree with *E. carlgreni* nom. nov. (≡*E. pallida* Carlgren, 1921). Should *E. delapiae* and *E. carlgreni* prove to be synonyms, the former name would have priority over *E. carlgreni* as the replacement name for *E. pallida*. See also *E. tecta* Haddon, an older possible synonym (appendix III). Distribution: southern Ireland.

*E. armata* Carlgren, 1931. Distribution: Fiji.

*E. bocki* Carlgren, 1931. Distribution: Fiji.

*E. duodecimtentaculata* Carlgren, 1931. Distribution: Fiji.

*E. gilbertensis* Carlgren, 1931. Distribution: Gilbert Islands, Great Barrier Reef.

*E. japonica* Carlgren, 1931. Distribution: eastern Japan.

*E. maroccana* Carlgren, 1931. Distribution: Morocco.

*E. octoradiata* Carlgren, 1931. Distribution: Japan.

*E. capensis* Carlgren, 1938. Distribution: southern South Africa.

*E. sanctaehelenae* Carlgren, 1941. Distribution: Saint Helena.

*E. norvegica* Carlgren, 1942. Distribution: Norway.

*E. annamensis* Carlgren, 1943. Distribution: Cambodia.

*E. stephensoni* Carlgren, 1950b. Certain aspects of this species agree with *E. bocki* Carlgren, 1931 and the two species may be synonymous. Distribution: Great Barrier Reef.

*E. vivipara* Carlgren, 1950c. Distribution: southern Australia.

*E. jonesii* Seshaiya and Cuttress, 1969. Distribution: southern India.

*E. ivelli* Manuel, 1975. Distribution: southern England.

*E. carlgreni* nom. nov. Senior objective synonym: *E. pallida* Carlgren, 1921 (*q.v.*). Distribution: Sweden.

*E. meridionalis* sp. nov. Synonym:? *E. intermedia* (*pro parte* (?) *sensu* Carlgren, 1899, 1927a, 1959); *non E. intermedia* McMurrich, 1893 (*q.v.*). Distribution: Ross Sea and South America (?).

## APPENDIX III

## INVALID NOMINAL *EDWARDSIA* SPECIES

The 39 *nomina clara* found amongst the published descriptions of nominal *Edwardsia* species have already been compared with *E. meridionalis*. The remaining nominal species comprise *nomina nuda, nomina dubia,* synonyms and homonyms considered to be invalid for the reasons shown below. However, if more detailed descriptions or type specimens applicable to these names could be found, some of them might be raised to the status of *nomina clara*.

### (1) Nomina nuda

*E. fischeri* Chevreux and de Guerne, 1887. This species has apparently never been described (see Fischer, 1887, p.432 and 1890, p.311). Although Fischer (1887, 1890) attributed the name to Chevreux and de Guerne, no other reference to *E. fischeri* was found in the literature.

*E. lucifuga* Fischer 1887. Given by Fischer (1887, p.432) in a geographical distribution list but the name was not made available until the next year (Fischer, 1888).

(2) Nomina dubia

*E. clavata* (Rathke, 1843). This species (≡*Actinia clavata* Rathke, 1843) was considered to be a senior synonym of *E. tuberculata* Düben and Koren by Andres (1883) and Carlgren (1893). Later, however, Carlgren (1921) rejected it as a *nomen dubium*, retaining *E. tuberculata* as a potentially valid name. Apparently Rathke (1843) did not record the presence of nemathybomes so the species may not be an *Edwardsia*. *E. clavata* (Rathke, 1843) is therefore not regarded as a secondary homonym of *E. clavata* Stimpson, 1855.

*E. brevicornis* Stimpson, 1855. This species cannot be identified with or differentiated from other *Edwardsia* species. Indeed, Verrill at first (1865) considered it to be a *Halcampa* Gosse, 1858a. (He mis-spelt the name as *Halocampa.)* Carlgren (1949) doubtfully included this species in the genus *Haloclava* Verrill, 1899, but Verrill had already himself (1899) suggested that the species belonged to *Eloactis* Andres, 1883.

*E. clavata* Stimpson, 1855. The description of this species is also inadequate to be certain of the genus to which it belongs. Verrill (1865) considered that it should be referred to the genus *Phellia* Gosse, 1858b. However, the species was transferred to the genus *Telmatactis* Gravier, 1916 by Carlgren (1949). It is not regarded here as a homonym of *E. clavata* (Rathke, 1843) (see above) so it does not require a replacement name at present.

*E. collaris* Stimpson, 1855. The same argument applies to this species as to *E. clavata* Stimpson. Again, Verrill (1865) considered it to be a *Phellia*, but Carlgren (1949) provisionally referred it to *Telmatactis* Gravier, 1916.

*E. cretata* Stimpson, 1855. The description is inadequate to identify or differentiate this species from other *Edwardsia* species and it is also doubtful whether it is an *Edwardsia*. Carlgren (1949), with some doubt, admitted the species to the genus *Paraedwardsia* Carlgren, 1905.

*E. rubricollum* Stimpson, 1855. This is probably not an *Edwardsia* species, since it was described as having a tuberculate margin and being attached to stones. Verrill (1865) defined a new genus *Ammonactis* for it; Fischer (1890) cast doubt on its validity, although Andres (1883) had accepted it without comment. Carlgren (1949) did not list *Ammonactis* Verrill, 1865 as an accepted genus of anemones or as a synonym of one.

*E. allmanni* McIntosh, 1865. Despite the subsequent publication of a coloured figure (McIntosh, 1875), this description is not adequate to identify this species with or differentiate it from any other (see Stephenson, 1935 and Manuel, 1975).

*E. goodsiri* McIntosh, 1865. The same argument and references apply to this species as to the foregoing.

*E. grubii* (A. Costa, 1869). This species, described originally as a sipunculid *Urophysalus grubii* A. Costa, was considered to be synonymous with *E. claparedii* (Panceri) by Andres (1883). However, although definitely an *Edwardsia*, it is not possible from the original description to allocate with certainty the anemone to any known species.

*E. arenosa* Klunzinger, 1877. Andres (1883) thought that this species might be a juvenile cerianthid, with which I would agree, but the description was brief and based only upon one specimen.

*E. coriacea* Moseley, 1877. Although the coloration of the single specimen found is well described, in the absence of any other remarkable physical features in the description, the species definition is inadequate. The coloration is, however, quite different from that of *E. meridionalis*.

*E. flaccida* Marion, 1882. This species was extremely briefly described and no useful diagnostic features were given.

*E. rigida* Marion, 1882. As for *E. flaccida* Marion.

*E. scabra* Marion, 1882. As for *E. flaccida* Marion.

*E. grubii* Andres, 1883. This species was poorly described and may not be an *Edwardsia*. Pax & Müller (1962) failed to rediscover it in the Adriatic Sea. Its name is here replaced by *E. perdita* nom. nov. (see p.351).

*E. octoplax* (Sluiter, 1888). Originally described as a gephyrean worm (*Diphtera octoplax*) by Sluiter (1888), the species was later recognised as an *Edwardsia* (Sluiter, 1889). The nemathybomes appear to occur in tightly packed groups and to possess one type of nematocyst (Sluiter, 1888, plate I). Not enough detail is given to confidently assign this species, however. The trivial name appears as both *oktoplax* and *octoplax* in the original description, but the latter spelling is adopted here.

*E. tecta* Haddon, 1889. The species is of uncertain status but if it proves to be the young of *E. delapiae* Carlgren and Stephenson, 1928, as suspected by Stephenson (1935), the name will be a senior synonym of *E. delapiae* (*q.v.* in appendix II).

*E. costata* Danielssen, 1890. This species was described as having papillae upon its eight ribs from the capitulum down to the physa. Although almost certainly an edwardsiid species, it is difficult to be certain to which genus it belongs.

*E. intermedia* McMurrich, 1893. The single type specimen was incompletely described and probably poorly preserved since the nemathybomes contained no nematocysts. This species has already been discussed in detail (pp. 342-344).

*E. ignota* Stuckey, 1909. The species, though poorly described, was said to have a naked scapus and hence may not be an *Edwardsia*.

*E. mammillata* Bourne, 1916. No useful diagnostic features were given for this species.

*E. rekaiyae* Bourne, 1916. As for *E. mammillata* Bourne.

*E. rugosa* Bourne, 1916. As for *E. mammillata* Bourne. The single type specimen was largely decomposed.

*E. vermiformis* Bourne, 1916. As for *E. rugosa* Bourne.

*E. willeyana* Bourne, 1916. As for *E. mammillata* Bourne.

*E. incerta* Carlgren, 1921. This species was described from a single imperfect and badly preserved specimen. The large scattered nemathybomes, however, distinguish the species from *E. meridionalis*.

(3) Synonyms
(a) Species-group synonyms.

*E. harassi* de Quatrefages, 1842. A junior subjective synonym of *E. timida* de Quatrefages, 1842 (see Dixon, 1886).

*E. farinacea* Verrill, 1869. A junior subjective synonym of *E. duodecimcirrata* Sars, 1851 (*q.v.*) (Andres, 1883; Carlgren, 1893, 1949) and a senior subjective synonym of *E. lutkenii* Andres, 1883 (*q.v.*) (Carlgren, 1893).

*E. grubii* Andres, 1883. A senior objective synonym of its replacement name *E. perdita* nom. nov. (see p.351).

*E. lutkenii* Andres, 1883. A junior subjective synonym of *E. duodecimcirrata* Sars, 1851 (*q.v.*) and of *E. farinacea* Verrill, 1869 (*q.v.*) (Carlgren, 1893).

*E. adenensis* Faurot, 1895. A junior subjective synonym of *E. pudica* Klunzinger, 1877 (see Carlgren, 1949).

*E. elegans* Farquhar, 1898. A senior objective synonym of its replacement name *E. tricolor* Stuckey, 1909 (see Stuckey, 1909) and, according to Carlgren (1924), a subjective synonym of *E. neozelanica* Farquhar, 1898.

*E. leidyi* Verrill, 1898. A junior subjective synonym of *E. lineata* Verrill, 1873 (*q.v.*) (see Crowell, 1976).

*E. tricolor* Stuckey, 1909. A junior subjective synonym of *E. neozelanica* Farquhar, 1898 and a junior objective synonym of *E. elegans* Farquhar, 1898 (see Carlgren, 1924).

*E. pallida* Carlgren, 1921. A senior objective synonym of its replacement name *E. carlgreni* nom. nov. (see p.351 and appendix II).

*E. callianthus* Rawlinson, 1935. A junior subjective synonym of *E. timida* de Quatrefages, 1842 (see Manuel, 1977) and also, therefore, of *E. harassi* de Quatrefages, 1842 (*q.v.*).

(b) Nominal *Edwardsia* species transferred to other genera.

*E. vestita* Forbes, 1843. A junior subjective synonym of *Pachycerianthus solitarius* (Rapp, 1829) (see Andres, 1883; Pax and Müller, 1962).

*E. sarsii* Düben and Koren, 1847. Transferred to the genus *Paraedwardsia* Carlgren, 1905 (see Carlgren, 1921, 1949).

*E. duodecimcirrata* Sars, 1851. Transferred to the genus *Halcampa* Gosse, 1858a (see Andres, 1883 and Carlgren, 1893; see also its junior subjective synonyms *E. farinacea* Verrill and *E. lutkenii* Andres).

*E. callimorpha* (Gosse, 1853). Reinstated in the genus *Scolanthus* Gosse, 1853 (see p.327),but *E. callimorpha (sensu* Stephenson, 1935) is synonymous with *E. claparedii* (*q.v.*), being a misidentification.

*E. sphaeroides* (Holdsworth, 1855). Originally described as *Scolanthus sphaeroides* Holdsworth, and at first transferred to the genus *Edwardsia* by Gosse (1855b). Later (Gosse, 1860) was regarded as a synonym of *Sagartia troglodytes* (Price *in* Johnston, 1847), a view shared by Stephenson (1935).

*E. carnea* Gosse, 1856. Transferred first to the genus *Edwardsiella* by Andres (1883) and later to *Milneedwardsia* Carlgren, 1893 (see Stephenson, 1935), which name being preoccupied, was replaced by *Fagesia* Delphy, 1938. However, as Crowell (1976) has pointed out, the name *Fagesia* is also preoccupied and a further replacement name is required. Meanwhile, *Fagesia* remains in use (*sensu* Carlgren, 1949). The *E. carnea* of Appellöf (1891) was, according to Carlgren (1921), a misidentification of *Paraedwardsia sarsii* (Düben and Koren, 1847).

*E. microps* (Gosse, 1858b). This species ( ≡ *Halcampa microps* Gosse) was regarded by Andres (1883) as an immature *Edwardsia*. Now known to be the young of *Fagesia carnea* (Gosse, 1856) (see Stephenson, 1935).

*E. lineata* Verrill, 1873. Currently known as *Fagesia lineata* (See Carlgren, 1949), but see note on *E. carnea* above.

*E. kerguelensis* Studer, 1878. Regarded as an *Edwardsiella* by Andres (1883) and later transferred to the genus *Halianthella* Kwietniewski, 1896 (see Carlgren, 1949).

*E. pallida* Verrill, 1879. Transferred to the genus *Drillactis* Verrill, 1922 (see Verrill, 1922).

*E. janthina* Andres, 1881. Andres (1883) reduced this nominal species to a variety of *E. claparedii* (Panceri, 1869). However, because of its external appearance and its natural habitat in holes in rocks (see Andres, 1883, plate 11), it is here transferred to the genus *Fagesia* Delphy, 1938. Further research may show *F. janthina* (Andres) to be synonymous with *F. carnea* (Gosse).

*E. lucifuga* Fischer, 1888. Transferred to *Isoedwardsia* Carlgren, 1921 (see Carlgren, 1949) but now regarded as a junior subjective synonym of *Scolanthus callimorphus* Gosse, 1853 (see p.327).

*E. horstii* Pax, 1924b. Carlgren (1931) examined the type material and found it to consist of specimens of both *Capneopsis solidago* Duchassaing and Michelotti, 1866 and *Isoedwardsia curacaoensis* Pax, 1924b. Hence, discounting the previously described *C. solidago*, *E. horstii* and *I. curacaoensis* are simultaneously published synonyms for the same taxon: since this taxon is a species of *Scolanthus* Gosse, 1853, the valid name adopted here is *S. curacaoensis* (Pax, 1924b).

*E. leucomelos* Parry, 1951. Transferred to the genus *Drillactis* Verrill, 1922 (see Carlgren, 1954). (Carlgren mis-spelt the trivial name as *leucomeles*.)

(4) Homonyms

*E. grubii* Andres, 1883 is a junior secondary homonym of *E. grubii* (A. Costa, 1869). The replacement name *E. perdita* nom. nov. is proposed for *E. grubii* Andres since there seem to be no available synonyms. The new trivial name refers to the apparent absence of records of this nominal species since it was first described by Grube (1864, p.107) as an un-named species.

*E. elegans* Farquhar, 1898 is a junior primary homonym of *E. elegans* Verrill, 1869. Stuckey (1909) proposed the replacement name *E. tricolor,* which is now rejected in favour of *E. neozelanica* Farquhar, 1898, since Carlgren (1924) considered *E. elegans* Farquhar and *E. neozelanica* Farquhar to be synonymous. If future work should show these two nominal species to be separate, then the name *E. tricolor* would be reinstated.

*E. pallida* Carlgren, 1921 is a junior primary homonym of *E. pallida* Verrill, 1879 (≡*Drillactis pallida* (Verrill, 1879) ). The replacement name *E. carlgreni* nom. nov. is proposed for *E. pallida* Carlgren since there appear to be no available synonyms.

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sipunculoides, Edwardsia........ **339**, 334, **346**.
*sipunculoides, Edwardsiella*........ **346**.
solidago, Capneopsis........ **350**.
solitarius, Pachycerianthus........ **350**.
*sphaeroides, Edwardsia*........ **350**.
*sphaeroides, Scolanthus*........ **350**.
Spiophanes........ **338**.
stephensoni, Edwardsia........ **342**, **347**.
sulcata, Edwardsia........ **339**, **346**.
tcherniai, Spiophanes........ **338**.
*tecta, Edwardsia*........ **349**.
*Telmatactis*........ **348**.
timida, Edwardsia........ **339**, **346**, 347, 349-350.
*timida, Edwardsia*........ **346**.
*timida, Edwardsiella*........ **346**.

tinctrix, Edwardsia ........................................ **341, 346.**
*tricolor, Edwardsia* ........................................ 341, 346, **349, 351.**
troglodytes, Sagartia .................................... **350.**
tuberculata, Edwardsia ................................. **339, 346,** 348.
*Urophysalus*................................................ **326-327,** 348.
vectensis, Nematostella ................................ **342.**
vegae, Edwardsia.......................................... **341, 347.**
*vermiformis, Edwardsia*................................ **349.**
*vestita, Edwardsia* ........................................ **350.**
vitrea, Edwardsia .......................................... **342, 346.**
*vitrea, Edwardsioides*.................................... **346.**
vivipara, Edwardsia ....................................... **342, 347.**
*willeyana, Edwardsia* .................................... **349.**

Manuscript accepted for publication 12 July, 1979.

# A NEW SPECIES OF THE BRACHIOPOD *NOTANOPLIA* (NOTANOPLIIDAE) FROM THE EARLY DEVONIAN OF NEW SOUTH WALES

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## SUMMARY

*Notanoplia mitchelli* sp. nov., a new notanopliid brachiopod, is described from Bowning, N.S.W., probably from the Lochkovian (Early Devonian) Elmside Formation. The distinctive genus is known only from Early and Middle Devonian rocks, and is known from Australia and Western Europe, and possibly from China.

## INTRODUCTION

Among collections purchased in 1930 by the Australian Museum are a number of brachiopods mostly labelled simply "Bowning". This material was collected by John Mitchell in the Yass, N.S.W., area in the years between 1883 and his death in 1928 (Brown, 1941). A few specimens belong to *Notanoplia* and constitute the basis of this paper; they appear to have previously received no more than passing attention. Nevertheless, in (presumably) Mitchell's handwriting, a label on the rock bearing one specimen (AMF 28650) bears the word "new". Another rock (bearing AMF 28873) bears the caption "*Stropheodonta*", reflecting Mitchell's broad concept of that genus (e.g. Mitchell, 1923). Other brachiopods curated with the above specimens — and possibly from the same formation — include mainly *Plectodonta bipartita* Chapman (= *P. davidi* Brown, 1949; see Savage, 1974, p.27), but inarticulate and orthacean brachiopods also occur.

The lithology, which is fine brown to grey mudstone, suggests that this material was from one of Mitchell's Upper Trilobite Bed localities. The problem of relating specimens to Mitchell's individual localities at Bowning has been discussed elsewhere (Sherwin, 1972), and appears to be insurmountable. Nevertheless, the label "Bowning" on specimens, the lithology and general fauna all point to the "Upper Trilobite Bed". Now assigned to the Elmside Formation (Link, 1970), the Upper Trilobite Bed (Mitchell, 1886) is placed at the same stratigraphic level as the algal limestones which yielded an *Icriodus woschmidti* conodont fauna (Link, 1970; Link and Druce, 1972); Klapper (1977, p.40) has suggested that the Yass *I. woschmidti* is more correctly *I. woschmidti hesperius*. The thickness of the Formation (Link, 1970, Fig. 1) appears to be about 20 m and the algal lenses occur towards the top of the unit (Link and Druce, 1972, Fig. 2). As the *I. woschmidti hesperius* occurrence is of earliest Devonian age (Klapper, 1977) this appears to be the most accurate age that can presently be inferred for the *Notanoplia* occurrence at Bowning. Mitchell (1923, p.470) and Gill (1953) had noted earlier the possibility of a Devonian age for the Upper Trilobite Bed. Lower parts of the Formation may be Pridolian (latest Silurian). The present occurrence supports the hypothesis that all *Notanoplia* are post-Silurian.

Collection of further material is considered unlikely, as fossiliferous outcrops of this "Bed" are sparse. However, I have seen no notanopliid from the lower horizons in the Yass Basin, and have been informed by the late Ida Browne and by K. S. W. Campbell and D. Strusz (pers. comm.) that they have seen no other *Notanoplia* from this area.

Records of The Australian Museum, 1981, **Vol. 33 No. 7**, 361-368, Figure 1.

## TAXONOMY

### Family Notanopliidae Gill, 1969

Type Genus: *Notanoplia* Gill, 1950.

REMARKS: When erected in 1969, the family was restricted to Australia and included *Notanoplia* and *Boucotia* Gill, 1969. Since then the concept and geographic range of this distinctive family has been extended by the following occurrences. Boucot and Johnson (1972) described *Callicalyptella* from the Early Devonian of Nevada and assigned *Hollardiella* Drot, 1966 from the Devonian of the Sahara to the family. Johnson (1973) described *Notoparmella,* also from the Early Devonian of Nevada. At almost the same time Havlicek (1973) described *Plicanoplia* (*non* Boucot and Harper, 1968) from the Early Devonian of Bohemia, which he re-named *Plicanoplites* in 1974. Havlicek (1977) described the new notanopliid genera *Serrulatrypa* and *Imatrypa* from Bohemia. The former genus was based on a notanopliid, *Boucotia incognita*, previously described by Langenstrassen (1972) from Germany along with some other notanopliids. It is important to note that some of the German and Bohemian occurrences are of Middle Devonian age. Xu Han-kui (1977) has described a number of Middle Devonian genera, from the province of Guangxi, China; those placed in the Notanopliidae (sic.) were *Costanoplia, Paracostanoplia* and *Luofuia*. Xu Han-kui also introduced the new family Plicanoplidae for *Plicanoplia* Havlicek (see above) and *Paraplicanoplia*.

Although notanopliids occur widely in Early Devonian rocks, they rarely occur in sufficient numbers to permit definition of variation. This has implications at both specific and generic levels where there is difficulty in delimiting the morphology of taxa. Morphological features which I consider poorly known include the septa and ornamentation. Some of the above genera therefore will probably need reconsideration in the future.

Other interesting recent reports of this group are by Bourque (1977, pl. 24, Fig. 4-13), who has recorded *Boucotia* from Gaspé Peninsula, and by Boucot and Potter (1977, p.211), who recorded *Notoparmella* from Northern California; both occurrences are from Early Devonian sequences. It is further noted that *Notoparmella* occurs in New Zealand and Victoria, in Siluro-Devonian and Silurian strata respectively (M. J. Garratt, pers. comm. concerning Victoria).

Reports of notanopliids from the U.S.S.R. are, thus far, inconclusive. *Notanoplia ganinensis* (Gratsianova, 1967, p.52, Fig. 15, pl. 3, Figs. 17-19; see also Alekseeva *et al.*, 1970, p.36, pl. 3, Figs. 1, 2) does not closely resemble typical notanopliids and is here considered to belong outside the Notanopliidae. It should be noted in this context that the ordinal affinities of this family are not certain, although recent opinions (Havlicek, 1973; Johnson, 1973) favour inclusion with the atrypaceans, normally classified as spiriferids.

### **Notanoplia** Gill, 1950

?1977 **Costanoplia** Xu Han-kui, p.65

Type Species: *N. pherista* Gill, 1950

DISCUSSION: The Bowning material is placed in *Notanoplia* rather than *Boucotia* as it lacks crestsepta considered by Gill (1969) to be characteristic of *Boucotia*. Although Xu Han-kui (1977, p.64) shows *Notanoplia* and *Boucotia* as being smooth, the presence of faint costellae in members of these genera is well established (Philip, 1962; Gill, 1969; Langenstrassen, 1972). Therefore *Costanoplia* Xu Han-kui is probably a synonym of *Notanoplia*.

### **Notanoplia mitchelli** sp. nov.

Fig. 1.

MATERIAL: Holotype, AMF 28650; paratypes AMF 29124, AMF 28873, AMF 29123a, AMF 29123b; ? AMF 28649. All from Bowning; presumably from the Upper Trilobite Bed of Mitchell (now placed in the Elmside Formation) of Lochkovian age.

DERIVATION OF NAME: The specific name records the outstanding contribution of the late John Mitchell to the geology of New South Wales.

DIAGNOSIS: *Notanoplia* with weakly ventri-biconvex shell, multiseptate pedicle interior and brachial valve with short peripheral septa. External ribs low and rounded.

DESCRIPTION: Weakly ventri-biconvex; brachial valve almost planar, especially antero-laterally. Outline sub-pentagonal to almost semi-circular; maximum width at about mid-length. Hingeline straight, nearly maximum width.

External ornamentation very weakly costellate, with closely spaced, faint growth lines (AMF 28873).

Pedicle interior dominated by robust median septum. Two further "principal septa" enclose slightly less than 90°; between these are up to 8 radial ridges of varied lengths but concentrated near, rarely at, valve margin; septa rarely occur between "principal septa" and hingeline. Hinge teeth stout. Pedicle tube prominent, musculature not visible as separate scars.

Brachial valve bears a prominent median septum which is stoutest posteriorly; in the largest specimen (AMF 28873 — valve length 4 mm) about 7 very short radial septa occur near the periphery. Muscle field obscure, may be weakly impressed alongside posterior end of median septum. Socket ridges low, rounded and weakly divergent from the hingeline. Cardinal process relatively short and wide, strongly convex towards the pedicle valve (scroll-like).

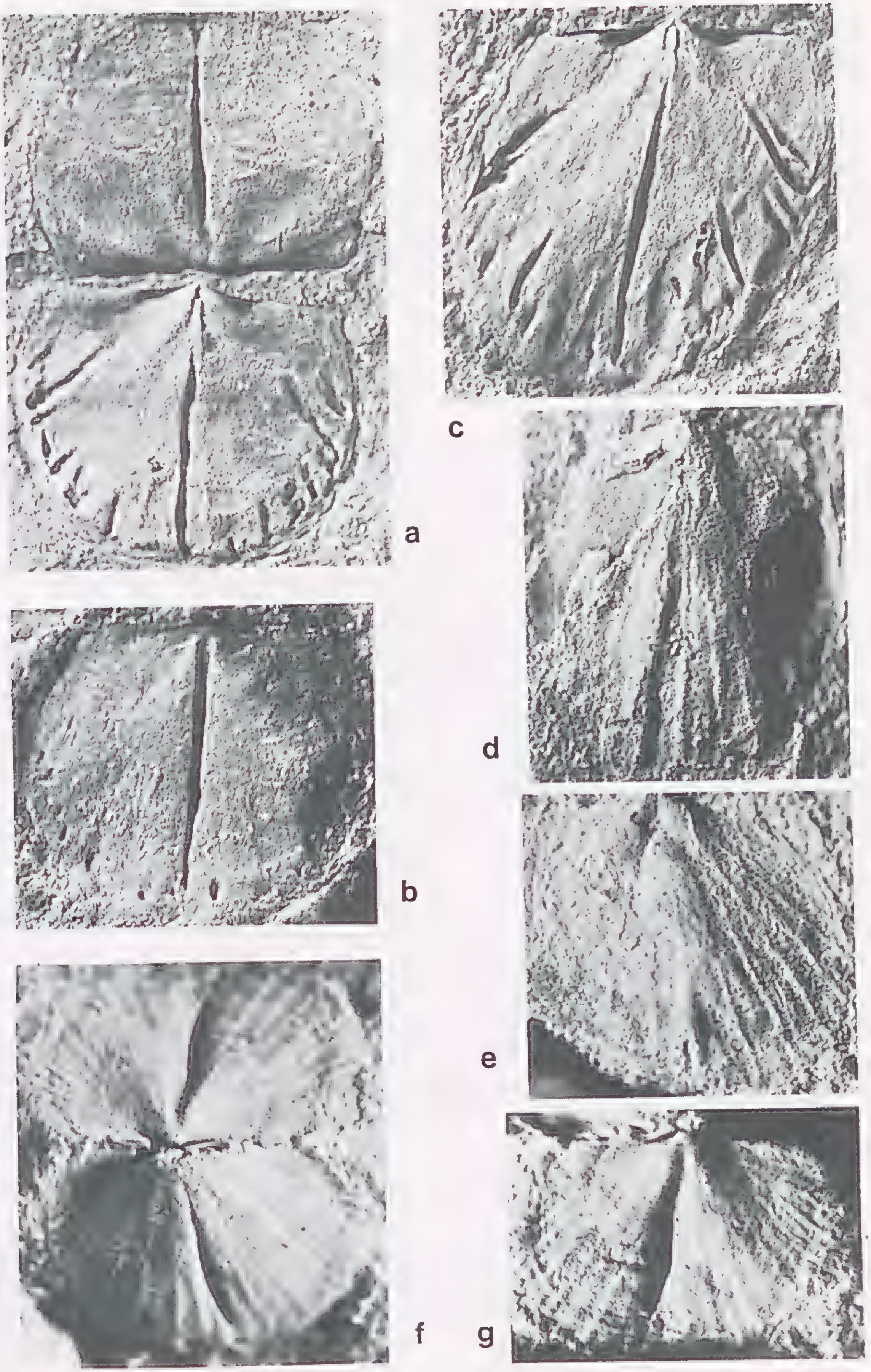
REMARKS: In addition to the above 5 specimens assigned to *N. mitchelli* sp. nov., the collection includes one further specimen (AMF 28649) which may belong there (Fig. 1, f-g). The specimen is an internal mould of an open bivalved juvenile shell (each is about 2.5 mm long) with a single weakly developed septum in each valve. In this latter aspect it differs markedly from AMF 28650 (the holotype) which, at a length of 3 mm for each valve, has well-developed peripheral septa in the pedicle valve.

The accessory septa in *N. mitchelli* sp. nov. are noteworthy in their almost haphazard development (Fig. 1). Further, in side view they are mostly short and seem to terminate in a spur directed anteriorly. The function of the septa may therefore have been as a barrier between external objects and the mantle cavity; Gill (1969, p.1228) has noted that where septa were developed in both valves of a single shell, the crests of the septa touched neither the crests nor the floor in the opposing valve when the valves were closed.

COMPARISONS: *N. pherista* (Gill, 1950, 1969) is characterised by poorly developed

Figure 1 — a-e. *Notanoplia mitchelli*, sp. nov. **a.** holotype AMF 28650, internal mould of both valves. **b.** paratype AMF 28873, internal mould of brachial valve. **c.** paratype AMF 29124, internal mould of pedicle valve. **d.** paratype AMF 29123a, partly testiferous pedicle valve. **e.** paratype AMF 29123b, external mould of pedicle valve. f-g.? *Notanoplia mitchelli* sp. nov., AMF 28649. **f.** view of internal mould of both valves, pedicle valve at foot of page. **g.** brachial valve.

All x 10 approximately except for **a** which is x 12 approximately.


a
b
c
d
e
f
g

lateral septa in the pedicle valve; its brachial valve contains the characteristic trifid septal pattern. In *N. mitchelli* sp. nov. the septa in the brachial valve are, except for the long, anteriorly bifurcating median septum, notably concentrated peripherally.

## STRATIGRAPHIC SIGNIFICANCE

Apart from the aforementioned Silurian *Notoparmella*, all known notanopliids are Devonian. That is, all strongly septate notanopliid genera are, as far as is known, good Devonian indicators. This appears to support the conclusion of Philip (1967) that the upper part of the Mt Ida Formation at Heathcote, Victoria is Devonian as it contains *Notanoplia*. However, the Silurian *Notoparmella* necessitates some reappraisal of the phylogeny proposed by Johnson (1973, text-fig. 2).

## ACKNOWLEDGEMENTS

It is a pleasure to acknowledge loan of this material by Dr A. Ritchie and Miss D. Jones. I also thank M. J. Garratt for discussion of the Notanopliidae, and Dr R. A. Facer for criticism of the manuscript.

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## NOTE ADDED IN PRESS

M. J. Garratt has drawn my attention to the discovery of true notanopliids in the U.S.S.R. (Gratsianova and Schischkina, 1977). Modzalevskaja *in* Rzonsnitskaja (1978) has described a further species from the U.S.S.R.

Xu Han-kui (1979) now considers that the age of the Tangxiang Formation, which yielded the notanopliids he described in 1977, is Early Devonian.

Savage *et al.* (1979, p.178) have listed some recently discovered notanopliids from North America.

Gratsianova, R. T., and G. R. Schischkina, 1977. On the ecology and distribution of the Devonian brachiopod family Notanopliidae. *Trudy Inst. Geol. Geofiz. sib. Otd.* 302; 22-29 [Russian].

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Manuscript accepted for publication 14 December, 1978.

# A NEW SPECIES OF *THYLOGALE* (MARSUPIALIA: MACROPODIDAE) FROM MAPALA ROCK SHELTER, JAYA (CARSTENSZ) MOUNTAINS, IRIAN JAYA (WESTERN NEW GUINEA), INDONESIA

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## ABTRACT

A new species of *Thylogale* (Marsupialia: Macropodidae) has been described on material from an archaeological deposit in Mapala rock shelter, situated at 3996 m in the Jaya Mountains, Irian Jaya, Indonesia. The remains of *Thylogale brunii* and several other mammal species are also present. The faunal material lies above a level dated at 5440 ± 130 BP, but the present status of either species of *Thylogale* in montane western New Guinea is unknown.

## INTRODUCTION

From December, 1971 to March, 1972, and in January and February, 1973, the Carstensz Glaciers Expeditions studied the tropical glaciers of the Jaya Mountains, Irian Jaya (western New Guinea), Indonesia. The results of these expeditions have been published by Hope *et al.* (1976). Although the aims of the expeditions were primarily glaciological and geomorphological, a small collection of faunal material was made, including a sample of bones salvaged from the floor of a rock shelter, discovered by an Indonesian mountaineering party. The bones formed part of an archaeological deposit in the rock shelter, and included the remains of a new species of *Thylogale*.

Mapala rock shelter lies at an altitude of 3996 m, close to Lake Larson, about 2 km north of the Northwall of Mt Jaya. It consists of a small overhang beneath a large block of limestone (15 x 15 x 8 m) perched by retreating ice on two small lateral moraine ridges. The site has been described in more detail by Hope, G.S. and Hope J.H. (1976). The archaeological deposit was discovered in February, 1972 when members of the Mapala Club of the University of Indonesia dug away part of the floor to provide more head room in the shelter, which was used as a camp site.

The first Carstensz Glaciers Expedition visited the Mapala camp and collected bulk samples of bone from the excavation spoil, and charcoal and a few bones from the face of the exposed section inside the rock shelter. Three distinct stratigraphic units were recognised in the deposit. The topmost 5 cm consisted of fine red-grey ash with no bone or charcoal. Beneath this was about 27 cm of a very black deposit, rich in bone, charcoal and carbonised twigs. The lowest layer consisted of about 10 cm of grey clayey silts with scattered bones and small fragments of charcoal. This horizon graded into a sterile grey silty clay containing pebbles; probably the basal limestone till. Charcoal fragments from the grey silts gave a $C^{14}$ date of 5440 ± 130 BP (ANU-1015).

The great majority of the bones collected came from the middle layer of the deposit, and apart from the species of *Thylogale* described below included the following: *Zaglossus bruijni, Dasyurus albopunctatus, Peroryctes longicauda, Pseudocheirus cupreus, P. mayeri, Phalanger* sp., *Thylogale brunii, Dendrolagus dorianus, Mallomys rothschildi, Hyomys goliath* and *Canis familiaris*. These remains, as well as collections of modern mammals from the area, have been discussed by Hope (1976). Other archaeological material from the deposit consisted of a fragment of a chert scraper, a piece of granodior-

Records of The Australian Museum, 1981, **Vol. 33 No. 8,** 369-387, Figures 1-7.

ite probably transported to the site by human agency, and several fragments of mollusc shell, including an indeterminate species of the family Geloinidae, which is restricted to brackish coastal waters.

### Family Macropodidae
### *Thylogale christenseni* sp. nov.
Figs. 1, 2

HOLOTYPE: AM F54719, left maxillary fragment, with P$^4$, M$^{1-4}$;
PARATYPES: AM F54718, cranial fragment, with right M$^{1-4}$;
AM F54727, right maxillary fragment, P$^3$, dP$^4$, P$^4$ unerupted (extracted), M$^{1-3}$, M$^4$ unerupted;
AM F54728, left maxillary fragment, P$^3$, dP$^4$, P$^4$ unerupted (extracted), M$^{1-3}$, M$^4$ unerupted;
AM F54729, left maxillary fragment, P$^3$, dP$^4$, P$^4$ unerupted (extracted), M$^{1-3}$, M$^4$ unerupted;
AM F54730, left mandibular ramus, lower incisor, P$_4$, M$_{1-4}$;
AM F54731, left mandibular ramus, lower incisor, P$_4$, M$_{1-4}$;
AM F54732, left mandibular ramus, lower incisor, P$_4$, M$_{1-4}$;
AM F54733, left mandibular ramus, P$_4$, M$_{1-4}$;
AM F54734, left mandibular ramus, lower incisor, P$_4$, M$_{1-4}$;
AM F54735, left mandibular ramus, P$_4$, M$_{1-3}$;
AM F54736, left mandibular ramus, P$_4$, M$_{1-4}$;
AM F54737, left mandibular ramus, P$_4$, M$_{1-4}$;
AM F54738, left mandibular ramus, M$_{1-4}$;
AM F54739, left mandibular ramus, M$_{2-4}$;
AM F54740, left mandibular ramus, M$_{1-3}$;
AM F54741, left mandibular ramus, M$_{1-4}$;
AM F54742, left mandibular ramus, lower incisor, P$_4$, M$_{1-4}$;
AM F54743, left mandibular ramus, dP$_4$, M$_{1-4}$;
AM F54744, left mandibular ramus, P$_3$, dP$_4$, M$_{1-2}$;
AM F54745, left mandibular ramus, P$_3$, dP$_4$, M$_{1-3}$;
AM F54746, left mandibular ramus, P$_3$, dP$_4$, M$_{1-2}$;
AM F54747, left mandibular ramus, M$_{1-2}$;
AM F54748, left mandibular ramus, M$_{1-3}$;
AM F54749, right mandibular ramus, lower incisor, P$_4$, M$_{1-4}$;
AM F54750, right mandibular ramus, lower incisor, P$_4$, M$_{1-4}$;
AM F54751, right mandibular ramus, P$_4$, M$_{1-4}$;
AM F54752, right mandibular ramus, P$_4$, M$_{1-4}$;
AM F54753, right mandibular ramus, M$_{1-4}$;
AM F54754, right mandibular ramus, M$_{3-4}$;
AM F54755, right mandibular ramus, M$_{1-2}$;
AM F54756, right mandibular ramus, M$_{1-4}$;
AM F54757, right mandibular ramus, lower incisor, P$_3$, dP$_4$, M$_{1-2}$;
AM F54758, right mandibular ramus, M$_{1-2}$;

TYPE LOCALITY: Mapala rock shelter, 4° 3′S, 137° 12′E, 3996 m altitude, 100 m southwest of Lake Larson, 2 km north of Northwall, Jaya Mountains, Sudirman Range, Irian Jaya, Indonesia.

LOCATION OF TYPE MATERIAL: The specimens have been registered in the palaeontological collection of the Australian Museum.

ORIGIN OF SPECIFIC NAME: This species is named for Ole Arne Christensen, a research student in Prehistory at the Australian National University, who studied archaeological rock shelters in the highlands of Papua New Guinea. He died in a road accident on December 16, 1974, shortly before a proposed trip to Irian Jaya to survey archaeological sites in the Mt Jaya region.

GENERIC ASSIGNATION: It is unfortunate that the upper incisors are not preserved in the material here described as *Thylogale christenseni,* since the position of the labial notch at or towards the back of $I^3$ is the main diagnostic character for the genus *Thylogale.* Apart from this, the teeth of *Thylogale* display fairly generalised macropodine characteristics, and fragmentary material can be assigned to the genus mainly by elimination of other possibilities.

The molars of *Thylogale* are rectangular, moderately high crowned, with poor to moderately developed midlinks. They differ on the one hand from the large high crowned molars of *Macropus* (s.l.), which usually have well developed midlinks, and on the other from the square, low crowned molars of the remaining New Guinea genera *Dorcopsulus, Dorcopsis* and *Dendrolagus.* Further, $M^1$and $M^2$ in *Dorcopsulus* and *Dorcopsis* have mesostyles posterolabially to the paracone, a character which is absent in *Thylogale.* The permanent upper premolar in *Thylogale* is large with a well-defined posterior labial cusp and usually a distinct lingual cingulum. It is longer relative to the molars than is the case in most species of *Macropus,* but is distinct from the very long, heavily ridged premolars of *Dorcopsis* and *Dorcopsulus.* A vestigal canine is occasionally present in *Thylogale,* but is never as well-developed as in *Dorcopsis* and *Dendrolagus.* On the basis of these characters the new species has been referred to *Thylogale* rather than to any of the other macropodid genera occurring in New Guinea.

SPECIFIC DIAGNOSIS: $p^4$ long and narrow, distinct posterior lingual cusp, poorly developed lingual cingulum; molars smaller than in any other species in the genus, weakly developed midlinks.

COMPARISON:

The type material of *Thylogale christenseni* has been compared in detail with specimens of *T. brunii* from Mapala rock shelter (AM F54759-54776; Figs 3, 4, 5); from Mt Giluwe, Papua New Guinea (CM15115-15122) and from the north slopes of Mt Wilhelm, Papua New Guinea (CM 15123); and with *Dorcopsulus vanheurni* from Mt Wilhelm, Papua New Guinea (CM 15124; Figs 6, 7). These latter specimens are in the collection of the CSIRO Division of Wildlife Research, Canberra. The material has also been compared with specimens of *T. thetis, T. stigmatica* and *T. billardierii* from Australia. Nomenclature follows Kirsch and Calaby (1977).

DESCRIPTON:

*Cranium:* The cranium is best preserved in F54718. It consists of the right premaxilla and maxilla, with the anterior part of the orbit, including the lachrymal, the posterior part of both frontals and part of the right jugal. The masseteric process is large, extending to the crown of the molars. The skull is much smaller than in any comparative specimens of *Thylogale* available, and approaches that of *Dorcopsulus vanheurni.* Although the palate is broken, there is enough bone preserved lingual to the molar row to suggest that posterior palatal vacuities were present, and that large perforations existed behind them, similar to those found in the palate of *T. billardierii.*

*Incisors:* The upper incisors are not preserved in any specimen. In F54718 the lengths of the alveoli along the lingual margin are: $I^1$, 2.0 mm; $I^2$, 2.3 mm; $I^3$, 3.4 mm. The lower incisors are broad and lanceolate; the curve along the long axis is gentler than in *T. brunii,* and most similar to the situation in *T. billardierii.*

*Canine:* F54718 possesses a tiny alveolus for a canine just posterior to the premaxilla-maxilla suture. A similar alveolus is occasionally present in *T. billardierii*, although the canine itself is rarely retained.

*Upper premolars:* Measurements of the upper premolars of *T. christenseni* and *T. brunii* are given in Table 1. In this and later tables all teeth, both left and right have been measured, so it is possible that an individual animal may be represented twice in each set of data.

$P^3$ is represented by teeth from F54727, F54728, and F54729. It is about two-thirds the size of $P^4$. There are three cusps present on the sectorial crest, the median one being marginally lower than the posterior and anterior. There is a small posterior lingual cusp and a narrow lingual cingulum. Lateral ridging is much weaker than in *T. brunii*, and the lingual cusp and cingulum are very poorly developed compared with *T. brunii, thetis* and *stigmatica*. In *T. billardierii* the lingual cingulum is also poorly developed, but the posterior lingual cusp is prominent.

$P^4$ is in position only in F54719, but has been excavated from F54727, F54728, and F54729. It is a long and narrow tooth, almost as long as $P^4$ in *T. brunii* but considerably narrower. In morphology, it is more like $P^4$ in *T. billardierii* than in the other speices of *Thylogale*. Three cusps are present along the sectional crest (four in F547290) but they are much less prominent than in *T. brunii*. The anterior and posterior cusps are the most strongly developed, the intervening ones being very small. A sharp labial crest descends from the anterior cusp, but the posterior cusp has no equivalent; ridgelets from the intermediate and posterior cusps are less prominent. A posterior internal cusp, about two-thirds the height of the posterior cusp, extends about one-quarter the way along the tooth.

This cusp is well set-off, separated from the posterior cusp by a V-shaped valley. This is most clearly displayed in the unworn specimens excavated from F54727-54729. In other species of *Thylogale* the posterior internal cusp is connected to the posterior cusp by a lateral spur or ridge. This is most distinct in *T. thetis* and *stigmatica*, where the posterior cusp and its connecting spur form a ridge at right angles to the long axis of the premolar. *Thylogale brunii* and *T. billardierii* are more similar to *T. christenseni*, but in these the lateral spur tends to enclose a small posterior basin. In *T. christenseni* the lingual cingulum is extremely narrow, fading out completely anteriorly. In this respect *T. christenseni* differs considerably from *T. brunii, stigmatica* and *thetis*, all of which have heavy lingual cingula enclosing longitudinal basins, and is similar to *T. billardierii*, which also has a narrow lingual cingulum. In F54719 there is a very small antero-lingual cusp opposite the anterior cusp.

$dP^4$ is represented in F54727, F54728 and F54729. The tooth tapers anteriorly and bears a strong parastylar cusp. A slight anterior cingulum extends from the parastylar cusp two-thirds of the way across the anterior face of the tooth, so the labial side of the tooth is longer than the lingual side. In contrast, in *T. brunii* $dP_4$ is square, since this cingulum extends the width of the tooth anteriorly. In *T. christenseni* $dP^4$ is narrower relative to the molars than is the case in other species of the genus.

*Upper molars:* Measurements of the upper molars of *T. christenseni* and *T. brunii* are given in Table 2. The molars are rectangular in shape, in contrast to the almost square molars in *T. brunii*. They are smaller than in any other species of *Thylogale;* and are similar in size to the molars of *Dorcopsulus*. The midlink in *T. christenseni* is weak, and similar to the condition found in *T. billardierii*, rather than in *T. brunii, thetis* and *stigmatica*, all of which have well-developed midlinks. There is no sign of a forelink. There is a short

TABLE 1 UPPER PREMOLAR DIMENSIONS OF THYLOGALE CHRISTENSENI AND THYLOGALE BRUNII
(All measurements in millimetres)

| Specimen | $P_3$ | | | $dP_4$ | | | $P_4$ | | |
|---|---|---|---|---|---|---|---|---|---|
| | L | AW | PW | L | AW | PW | L | AW | PW |
| *Thylogale christenseni* | | | | | | | | | |
| AM F54719(holotype) | — | — | — | — | — | — | 6.4 | 2.2 | 2.6 |
| AM F54727 | 4.3 | 1.9 | 1.9 | 4.0 | 2.8 | 2.9 | 6.5 | 2.3 | 2.7 |
| AM F54728 | 4.3 | 1.9 | 2.0 | 4.2 | 2.7 | 2.8 | 6.3 | 2.0 | 2.6 |
| AM F54729 | 4.2 | 1.8 | 1.9 | 3.9 | 2.6 | 2.8 | 6.7 | 2.2 | 2.8 |
| *Thylogale brunii* | | | | | | | | | |
| Mapala Rock Shelter: | | | | | | | | | |
| AM F54759 | — | — | — | — | — | — | 6.8 | 3.0 | 3.2 |
| AM F54760 | 5.1 | 2.3 | 2.9 | 5.1 | 3.8 | 4.2 | 6.7 | 3.1 | 3.4 |
| AM F54761 | — | — | — | 4.6 | 3.6 | 3.8 | 6.4 | 3.1 | 2.9 |
| Mt Giluwe: | | | | | | | | | |
| CM 15115 | 4.9 | 2.3 | 2.7 | 5.1 | 3.6 | 4.1 | — | — | — |
| CM 15116 | 5.1 | 2.4 | 2.9 | 5.0 | 3.8 | 4.3 | 6.7 | 2.6 | 3.1 |
| CM 15117 | 5.2 | 2.4 | 3.0 | 5.1 | 3.9 | 4.2 | — | — | — |
| CM 15118 | 5.6 | 2.7 | 3.1 | 5.4 | 4.0 | 4.4 | — | — | — |
| CM 15119 | 5.2 | 2.5 | 3.1 | 5.1 | 3.9 | 4.2 | — | — | — |
| CM 15120 | — | — | — | — | — | — | 6.5 | 2.4 | 3.2 |
| CM 15121 | 5.3 | 2.6 | 3.1 | 5.4 | 3.9 | 4.5 | — | — | — |
| CM 15122 | 5.5 | 2.6 | 3.0 | 4.9 | 3.8 | 3.0 | — | — | — |
| Mt Wilhelm: | | | | | | | | | |
| CM 15123 | — | — | — | — | — | — | 7.8 | 3.2 | 3.8 |

## TABLE 2 UPPER MOLAR DIMENSIONS OF THYLOGALE CHRISTENSENI and THYLOGALE BRUNII
(All measurements in millimetres)

| Dimension | | *Thylogale christenseni* | | | | | *Thylogale brunii* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Mapala | | | | | Mt Giluwe | | Mt Wilhelm |
| | | 54718 | 54719 | 54727 | 54728 | 54729 | 54759 | 54760 | 54761 | N | X | S | O.R. | 15123 |
| | L | 4.0 | 4.0 | 4.0 | 4.4 | 4.3 | 5.1 | 5.3 | 5.1 | 8 | 5.28 | 0.18 | 5.0-5.6 | 5.5 |
| $M_1$ | AW | 3.5 | 3.5 | 3.2 | 3.4 | 3.1 | | 4.8 | 4.5 | 8 | 4.71 | 0.18 | 4.4-4.9 | 5.6 |
| | PW | 3.4 | 3.3 | 3.3 | 3.2 | 2.9 | | 4.9 | 4.4 | 8 | 4.61 | 0.27 | 4.0-4.8 | 5.4 |
| | L | 4.5 | 4.3 | 4.7 | 4.7 | 4.8 | 5.7 | 5.8 | 5.6 | 8 | 5.81 | 0.15 | 5.7-6.0 | 6.2 |
| $M_2$ | AW | 3.8 | 3.9 | 3.7 | 3.6 | 3.3 | 5.2 | 5.4 | 4.8 | 8 | 5.15 | 0.12 | 5.0-5.3 | 6.0 |
| | PW | 3.6 | 3.5 | 3.5 | 3.5 | 3.3 | 4.9 | 5.0 | 4.7 | 8 | 4.78 | 0.21 | 4.5-5.1 | 5.7 |
| | L | 5.0 | 4.7 | 4.9 | 5.0 | 4.9 | 6.4 | 6.4 | 6.2 | 6 | 6.17 | 0.25 | 5.8-6.5 | 7.2 |
| $M_3$ | AW | 4.0 | 3.9 | 3.7 | 3.8 | 3.7 | 6.0 | 5.9 | 5.1 | 6 | 5.13 | 0.20 | 4.9-5.4 | 6.5 |
| | PW | 3.6 | 3.4 | 3.6 | 3.6 | 3.5 | 5.1 | 5.2 | 4.5 | 6 | 4.60 | 0.09 | 4.5-4.7 | 5.2 |
| $M_4$ | L | 5.0 | 4.9 | | | | 6.2 | | | 2 | | | 6.2-6.3 | 6.7 |
| | AW | 3.8 | 3.7 | | | | 5.7 | | | 2 | | | 4.7-4.9 | 6.3 |
| | PW | 3.3 | 2.6 | | | | 4.6 | | | 2 | | | 4.1-4.2 | 4.5 |
| $M_{1-2}$ | | 8.7 | 8.4 | 8.7 | 9.1 | 9.0 | 10.8 | 11.2 | 10.9 | 8 | 11.16 | 0.23 | 10.8-11.5 | 11.8 |
| $M_{1-3}$ | | 13.6 | 13.1 | 13.3 | 14.0 | 13.7 | 17.3 | 17.7 | 17.1 | 6 | 17.20 | 0.32 | 16.6-17.4 | 18.9 |
| $M_{1-4}$ | | 18.6 | 18.0 | | | | 23.9 | | | 2 | | | 23.6-23.7 | 25.1 |

anterior cingulum, which extends only three-quarters of the way across the front of the molars. This contrasts with the condition in *T. brunii, thetis* and *stigmatica*, where the anterior cingula extend completely across, or almost so, and is again similar to *T. billardierii*.

*Lower premolars:* Measurements of the lower premolars of *T. christenseni* and *T. brunii* are given in Table 3. $P_3$ is a short narrow blade with three very faintly defined ridges on the labial and lingual sides.

$dP_4$ is similar to that of other species of the genus but the protoconid is greatly reduced.

$P_4$ is a narrow blade with up to four ridges on the labial and lingual faces. The anterior cusp is strongly defined. In other species of *Thylogale*, a crest descends anteriorly from the anterior cusp so that in lateral view the anterior face of the tooth is convex or angular; the crown length of the tooth being less than the length at the base of the enamel. In *T. christenseni*, however, the anterior face of the tooth is vertical in most cases, with only a few specimens showing an expansion anteriorly at the base of the enamel (e.g. F54732, F54751).

*Lower molars:* Measurements of the lower molars of *T. christenseni* and *T. brunii* are shown in Table 3. The lower molars are rectangular in shape with weakly developed fore and midlinks. The anterior cingulum does not extend as far across the face of the tooth as it does in other species of the genus. In size the molars are very similar to the lower molars of *Dorcopsulus*, but are higher crowned.

## DISCUSSION

This new species is consistent in all respects with the four modern species of *Thylogale*, and is quite distinct from the other macropodid genera represented in New Guinea. It is most similar to *T. billardierii* from Tasmania, so it is particularly regrettable that $I^3$ is not preserved, since *T. billardierii* is somewhat aberrant, compared to the other species of *Thylogale*, in that the labial notch does not extend as far towards the back of the tooth.

Most of the *Thylogale* specimens recorded from Australian fossil sites are of late Pleistocene or Holocene age and have been referred to one or other of the extant Australian species. However isolated teeth from the Hamilton Fauna recovered from Late Pliocene terrestrial deposits at Grange Burn, western Victoria, have been referred to the genus and are regarded as representing a new taxon (Turnbull and Lundelius 1970). This species is also similar in many respects to *T. billardierii*, but is of comparable size, so is much larger than *T. christenseni*. It is of interest that the Hamilton Fauna also contains material referred to the New Guinean taxa *Phalanger gymnotis* and *Dorcopsis* sp.

Two species of *Thylogale* have been previously recorded from New Guinea, the widespread *T. brunii* and *T. stigmatica*, known only from southwest Papua. Three subspecies of *T. brunii* are recognised; *T. brunii brunii* from Aru Island and southern New Guinea, *T. brunii browni* from the Bismarck Archipelago and the lowlands of northern New Guinea, as far west as Jayapura, and *T. brunii keysseri* from the Huon Mts and the highlands of Papua New Guinea (Tate 1948). By comparison with Tate's measurements, the specimens of *T. brunii* from Mapala rock shelter and Mt. Giluwe belong to the mountain subspecies *keysseri*, the smallest of the three. The measurements of specimen CM 15123, collected from an unknown altitude, possibly close the Ramu River, on the northern slopes of Mt. Wilhelm, agree with those given by Tate for the subspecies *browni*.

## TABLE 3 LOWER TEETH DIMENSIONS OF THYLOGALE CHRISTENSENI and THYLOGALE BRUNII
(All measurements in millimetres)

| Dimensions | | *Thylogale christenseni* | | | | *Thylogale brunii* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Mapala | | | | Mt Giluwe | | | | Mt Wilhelm |
| | | N | X | S | O.R. | N | X | S | O.R. | N | X | S | O.R. | 15123 |
| $P_3$ | L | 4 | 3.73 | 0.13 | 3.6-3.9 | 7 | 4.46 | 0.08 | 4.3-4.5 | 6 | 4.57 | 0.20 | 4.4-4.8 | |
| | AW | 4 | 1.45 | 0.10 | 1.3-1.5 | 7 | 1.69 | 0.11 | 1.6-1.9 | 6 | 1.82 | 0.10 | 1.7-1.9 | |
| | PW | 4 | 1.63 | 0.15 | 1.5-1.8 | 7 | 2.01 | 0.09 | 1.9-2.1 | 6 | 2.13 | 0.12 | 2.0-2.3 | |
| $dP_4$ | L | 4 | 3.45 | 0.06 | 3.4-4.5 | 9 | 4.39 | 0.09 | 4.3-3.5 | 6 | 4.65 | 0.15 | 4.4-4.8 | |
| | AW | 4 | 1.75 | 0.13 | 1.6-1.9 | 8 | 2.28 | 0.05 | 2.2-2.3 | 6 | 2.47 | 0.08 | 2.4-2.6 | |
| | PW | 4 | 2.03 | 0.05 | 2.0-2.1 | 9 | 2.84 | 0.09 | 2.7-2.9 | 6 | 2.97 | 0.19 | 2.7-3.2 | |
| $P_4$ | L | 9 | 5.44 | 0.27 | 5.1-5.9 | 4 | 6.18 | 0.21 | 6.0-6.4 | 2 | | | 5.8-6.3 | 7.4 |
| | AW | 9 | 1.70 | 0.09 | 1.6-1.8 | 4 | 2.28 | 0.31 | 2.0-2.7 | 2 | | | 1.9 | 2.3 |
| | PW | 9 | 1.70 | 0.09 | 1.6-1.8 | 4 | 2.38 | 0.43 | 1.9-2.9 | 2 | | | 1.9-2.1 | 2.4 |
| $M_1$ | L | 26 | 3.77 | 0.13 | 3.6-4.0 | 13 | 4.65 | 0.19 | 4.3-5.0 | 8 | 4.83 | 0.17 | 4.6-5.1 | 5.3 |
| | AW | 23 | 2.50 | 0.13 | 2.3-2.8 | 12 | 3.06 | 0.10 | 2.8-3.2 | 7 | 3.26 | 0.11 | 3.1-3.4 | 3.6 |
| | PW | 24 | 2.68 | 0.16 | 2.4-2.9 | 13 | 3.32 | 0.18 | 2.8-3.5 | 8 | 3.56 | 0.15 | 3.3-3.8 | 3.7 |
| $M_2$ | L | 28 | 4.14 | 0.18 | 3.8-4.4 | 14 | 5.34 | 0.20 | 4.9-5.7 | 8 | 5.33 | 0.12 | 5.2-5.5 | 6.1 |
| | AW | 26 | 2.99 | 0.15 | 2.8-3.5 | 13 | 3.79 | 0.13 | 3.6-4.0 | 8 | 3.79 | 0.29 | 3.1-4.0 | 4.3 |
| | PW | 27 | 3.10 | 0.15 | 2.9-3.4 | 14 | 3.94 | 0.17 | 3.6-4.2 | 8 | 4.09 | 0.19 | 3.8-4.3 | 4.3 |
| $M_3$ | L | 22 | 4.56 | 0.14 | 4.3-4.8 | 8 | 5.96 | 0.32 | 5.4-6.3 | 6 | 5.78 | 0.24 | 5.5-6.1 | 6.8 |
| | AW | 21 | 3.44 | 0.19 | 3.2-3.8 | 8 | 4.35 | 0.27 | 4.0-4.7 | 6 | 4.40 | 0.11 | 4.3-4.6 | 5.0 |
| | PW | 21 | 3.42 | 0.20 | 3.1-3.8 | 8 | 4.44 | 0.30 | 4.0-4.8 | 6 | 4.35 | 0.10 | 4.2-4.5 | 5.0 |
| $M_4$ | L | 17 | 4.66 | 0.23 | 4.3-5.0 | 5 | 6.38 | 0.33 | 5.9-6.7 | 2 | | | 6.3-6.6 | 7.5 |
| | AW | 16 | 3.44 | 0.20 | 3.2-3.8 | 5 | 4.76 | 0.23 | 4.4-5.0 | 2 | | | 4.5-4.6 | 5.2 |
| | PW | 17 | 3.14 | 0.21 | 2.7-3.6 | 5 | 4.32 | 0.32 | 3.9-4.7 | 2 | | | 4.1-4.3 | 4.6 |
| $M_{1-2}$ | | 26 | 8.08 | 0.23 | 7.6-8.5 | 13 | 10.02 | 0.25 | 9.6-10.5 | 8 | 10.36 | 0.22 | 10.1-10.8 | 11.0 |
| $M_{1-3}$ | | 19 | 12.67 | 0.35 | 12.0-13.2 | 7 | 15.99 | 0.45 | 15.5-16.7 | 6 | 16.27 | 0.12 | 16.1-16.4 | 17.6 |
| $M_{1-4}$ | | 15 | 17.53 | 0.41 | 16.8-18.1 | 4 | 22.48 | 0.48 | 21.8-22.9 | 2 | | | 23.0-23.8 | 24.3 |

The presence of *T. christenseni* in the Mapala rock shelter together with the widespread species *T. brunii* is surprising. In archaeological sites in montane areas of eastern New Guinea, *T. brunii* has been found together with *Dorcopsulus vanheurni* (White 1972). *Dorcopsulus vanheurni* is not represented in the Mapala site, and its closest known occurrence is at Mt Trikora (Wilhelmina), 150 km to the east. In 1939 the Third Archbold Expedition collected a series of 19 specimens at altitudes ranging from 850-2700 m in the region between Mt Trikora and the Tariku (Idenberg) River (Tate 1948); these remain the only specimens of *D. vanheurni* recorded from Irian Jaya. Faunal records for this region are in fact extremely poor, and the series of *Thylogale brunii* from Mapala represent the only record of the mountain subspecies *keysseri* in western New Guinea.

The Archbold Expedition to Mt Trikora neither saw nor collected any wallabies in the grasslands above 3000 m and remarked on the paucity of animals there (Archbold *et al.* 1942; Brass 1941). The experience of the Carstensz Glaciers Expeditions was similar. Mammals were rarely seen in the Mt Jaya region and the only species recorded living in the area were *Zaglossus bruijni, Peroryctes longicauda, Mallomys rothschildi, Rattus* spp., and wild dogs. No trace of wallabies was noted, and the local Damal people gave conflicting statements as to whether wallabies still live in the area.

The Mapala rock shelter lies towards the south of the Kemabu Plateau, an expanse of gently rolling country extending north from the sheer cliffs of the Northwall, the northern boundary of the rugged Jaya Mts. The Plateau extends about 500 km east-west and 25 km north-south, at altitudes between 3,400 and 4,200 m. The valleys on the plateau are covered with tussock grassland, while subalpine forest and shrublands grow on the ridge tops and extensive groves of tree ferns clothe the intervening slopes. There is some evidence that the present extent of the grasslands is due to human activity (mainly burning) over the last 10,000 years. Grasslands were much more extensive during cold phases of the late Pleistocene, when the maximum extent of the Mt Jaya ice cap was about 800 sq km. It is estimated that at the height of the last glaciation, mountain grassland covered about 16,000 sq km in the Sudirman Range (Mt Jaya and Mt Trikora areas) compared with about 4000 sq km at present (Hope, J. H. and Hope, G.S. 1976). There is no evidence about the nature of these grasslands from the Mt Jaya area itself, but if they resembled those of Papua New Guinea at that time, much of the area would have supported scattered shrublands, providing a varied, mosaic environment.

Relatively little is known about the ecology of the various species of *Thylogale*. Ziegler (1977:134) describes *T. brunii* as inhabiting 'man-made and alpine grasslands and areas of secondary growth, seldom straying far into thick forest'. The series of *T. brunii* from Mt Giluwe, in the western highlands of Papua New Guinea, was collected at an altitude of about 3,700 m, close to the summit. Mt Giluwe, a large strato-volcano, is mostly open grassland above about 3100 m. The wallabies came from very small forest patches not more than about 40 acres in extent (Newsome 1971). Wallaby dung was seen only in the grass close to these patches, and not elsewhere in the vast expanses of grassland or close to other forest patches. Newsome suggested that although the wallabies were not present in all forest patches, these patches were responsible for the survival of the species in the area.

In contrast, the other small wallaby of montane New Guinea, *Dorcopsulus vanheurni,* seems to be more characteristic of dense forest areas (Zeigler 1977). Specimens caught on Mt Wilhelm, PNG, came from relatively undisturbed areas of montane forest at about 2,700 m, well away from both the higher grasslands and the cultivated areas.

In Australia, *Thylogale thetis* and *T. stigmatica* occur in rainforest in coastal Queensland and northern New South Wales. Calaby (1966) recorded the species in the Clarence and Upper Richmond River areas of northern NSW. Here both species occurred in rain forest, in large patches of lantana on areas formerly covered with rain forest, and sometimes in wet gullies with a dense shrubby ground stratum, close to larger rain forest patches. The two species were not found together, the smaller rain forest patches being occupied by one species only, and where both occurred in a large patch, they occupied discrete areas. The ecological factors governing the distribution of the two species were not determined. Both species, however, came out of the rain forest and fed close to the edge in the evening.

The Tasmanian species, *Thylogale billardierii,* occurs in damp, densely vegetated areas such as fern gullies, the edges of rain forest and in drainage areas of heathland where the scrub is tall and dense (Green 1974). It emerges at dusk to feed on shrubs, native grasses and introduced pasture if this lies near its territory.

Given the similarity of habitat for the various species of *Thylogale,* that is, a dependence on forest or shrub patches, but with movement into more open vegetation on the edges of these patches for feeding, it is probably reasonable to assume that *T. christenseni* had similar habits. The presence of both *T. christenseni* and *T. brunii* together in a rock shelter on the Kemabu Plateau is an interesting parallel to the sympatric distribution of *T. thetis* and *T. stigmatica* in eastern Australia. In New Guinea, the shrub-rich grasslands with their patches of forest would seem to have provided a suitable habitat for species of *Thylogale,* both now and in the past. During the late Pleistocene, shrub-rich montane grasslands were more extensive on all the high mountain areas of New Guinea. The major reduction in grassland area that occurred after 14,000 BP would have put pressure on all species living in these areas. Mt Jaya, however, possesses the most extensive area of high plateau and would have been least affected, so most important as a refuge for high altitude populations. It is possible to speculate that *T. christenseni* may have once been more widespread in montane New Guinea, but after the expansion of forest between 14,000 and 10,000 years most islands of shrub-rich grassland were able to support only one species (*T. brunii*), while the larger expanse of the Kemabu Plateau (and possibly equivalent areas around Mt Trikora) were able to support two species, both *T. brunii* and *T. christenseni.*

Both *T. brunii* and *T. christenseni* certainly survived in the Mt Jaya area until less than 5000 years ago, but the question of whether either or both persist there today can only be answered by further field work. However, the lack of sightings of wallabies or their dung by the recent expeditions suggests that they must be fairly rare. While faunal records for the area are extremely sparse, the contrast between the extensive faunal list from the Mapala rock shelter and the few modern records does suggest that there has been some decrease in the mammal fauna within the last 5000 years. Pollen records for the Mt Jaya region suggest that clearance and burning by man within the last 10,000 years have partly reversed the development of high forest, and increased the extent of shrub-rich grassland and forest patches. Burning was probably at a peak between 2-3000 years BP (Hope, G.S. and Hope, J.H. 1976). The first effect of this may have been neutral or even favourable for the fauna, but burning would have been accompanied by hunting, and this, together with the advent of the dog, both feral and as a hunting aid, is the likeliest cause for the apparently rare (or possibly extinct) present status of the two thylogales. However, it should be noted that the small populations of *T. brunii* on Mt Giluwe have managed to survive in spite of a high density of feral dogs and native hunters. Dogs have probably been in New Guinea for only about 3000 years (Hope 1977), and the presence of the remains of one in the small sample from the Mapala rock shelter may be significant;

dog remains are relatively rare in eastern New Guinea archaeological sites, and have only been found in the very youngest levels (White 1972).

## CONCLUSION

*Thylogale christenseni* is recorded only from a single late Holocene deposit in Irian Jaya. It is not known whether the species still survives, either in Irian Jaya or Papua New Guinea. Consideration of its probable ecology and the past extent of suitable habitat suggests the possibility that it may once have been widely distributed in montane New Guinea. The parallelism with *T. billardierii* in many characteristics is interesting, in the light of Tasmanian-montane New Guinea relationships in general, which seem to reflect a similar ancestral fauna and flora related to that of the middle and late Tertiary of mainland Australia.

## ACKNOWLEDGEMENTS

I am grateful to the members of the Carstensz Glaciers Expedition, who collected the faunal material from Mapala rock shelter, and to Dr A. Newsome, for use of his specimens of *Thylogale brunii* from Mt Giluwe.

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Manuscript accepted for publication 27 April, 1979.

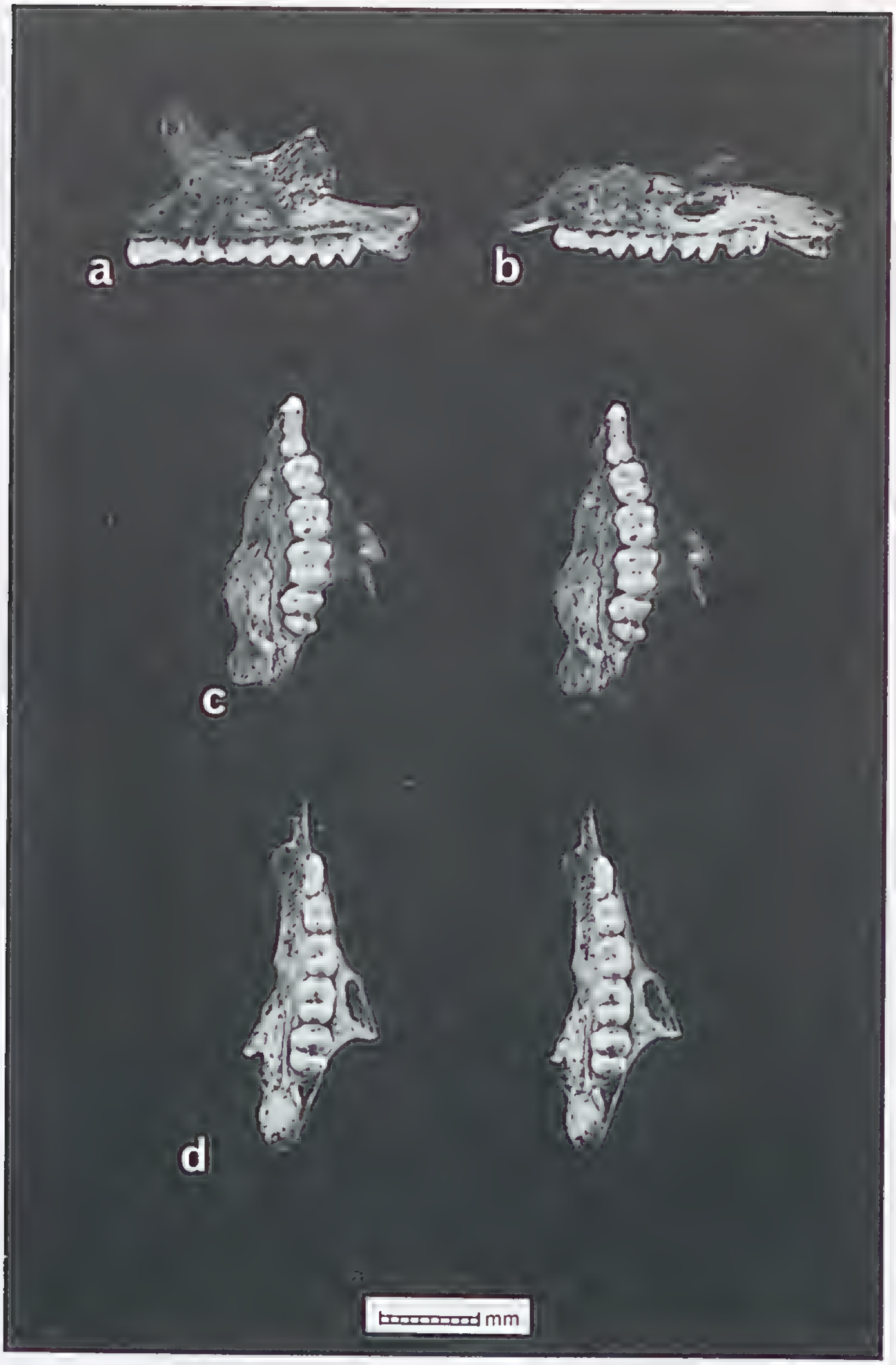

Fig. 1
*Thylogale christenseni* sp. nov.

Fig. 1a Lateral view of holotype, left adult maxilla, AM F54719.

Fig. 1b Lateral view of juvenile maxilla, AM F54728.

Fig. 1c Stereopair of occlusal view of holotype, AM F54719.

Fig. 1d Stereopair of occlusal view of AM F54728.

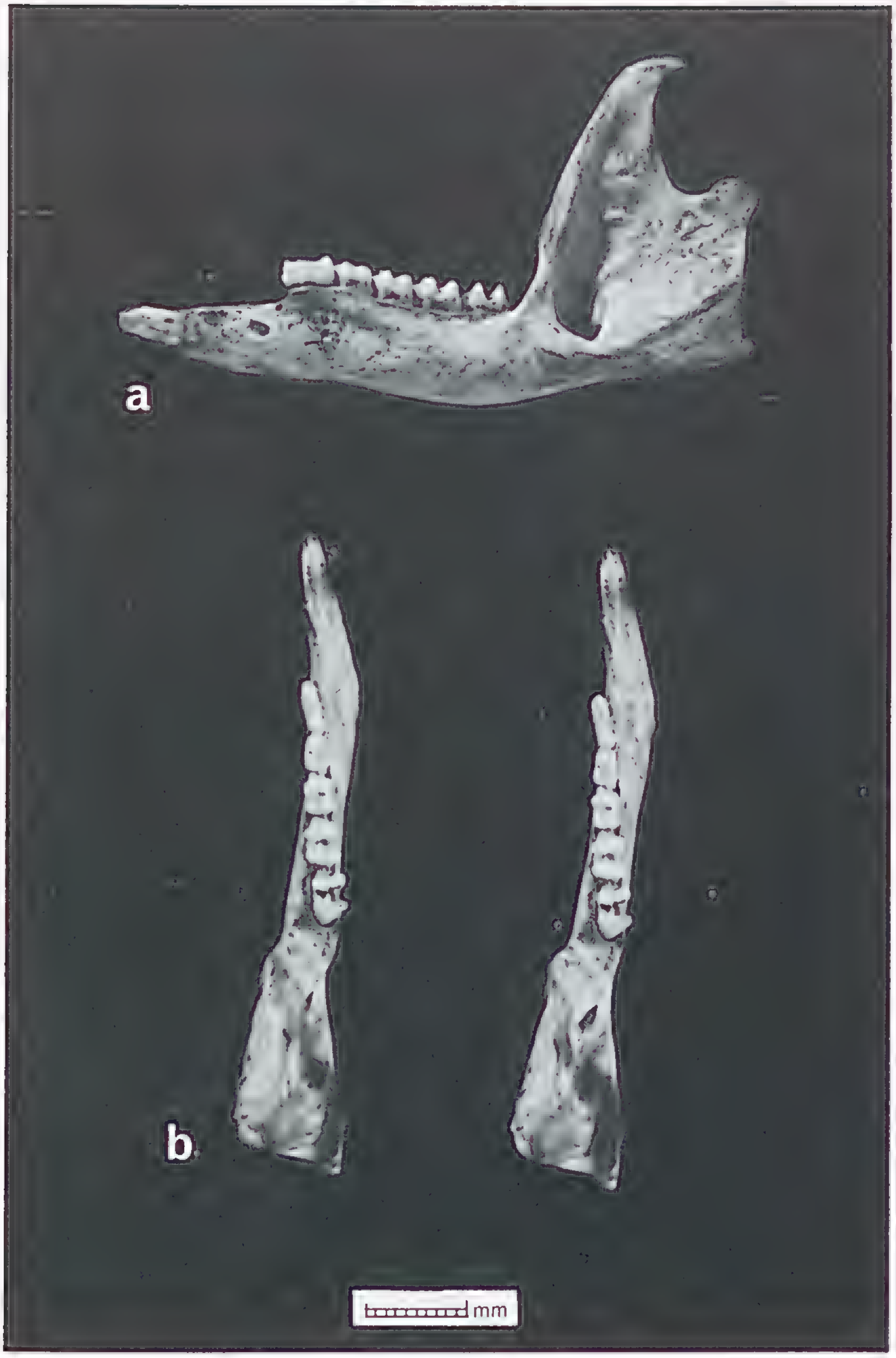

Fig. 2

*Thylogale christenseni* sp. nov.

Fig. 2a Lateral view of left adult mandibular ramus, AM F54730.

Fig. 2b Stereopair of occlusal view of AM F54730.

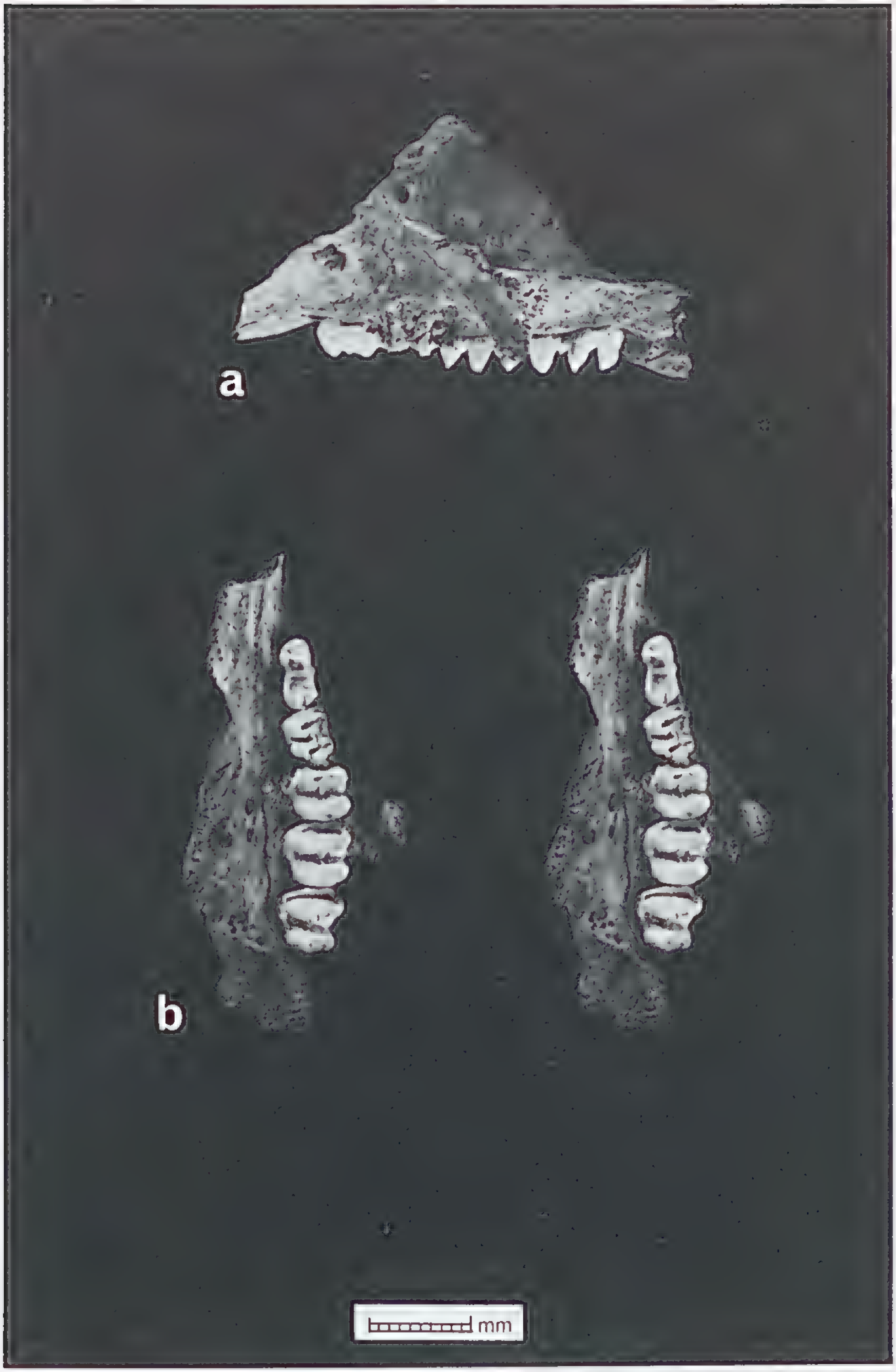

Fig. 3

*Thylogale brunii* (Schreber, 1778)

Fig. 3a Lateral view of left adult maxilla, AM F54759.

Fig. 3b Stereopair of occlusal view of AM F54759.

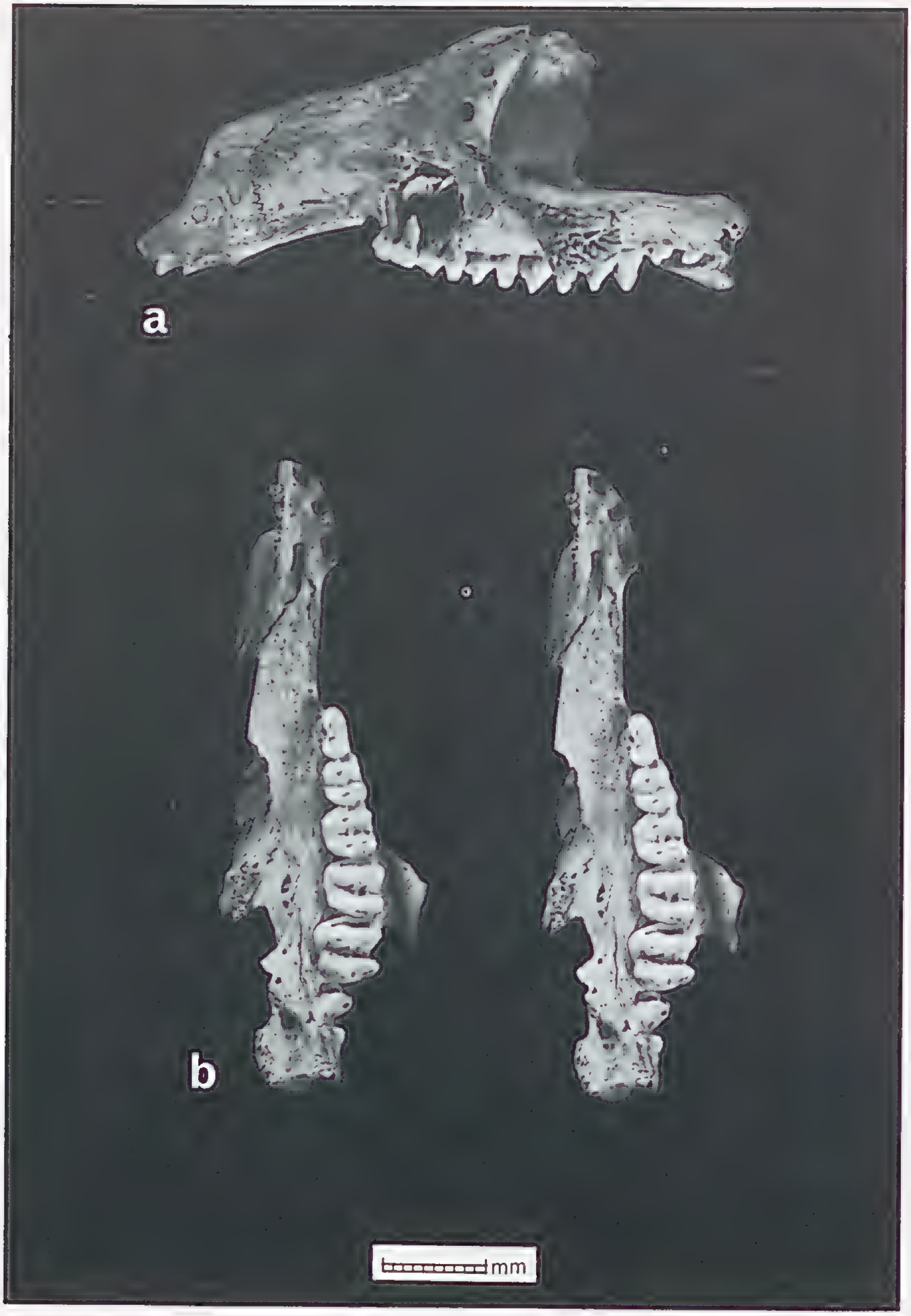

Fig. 4

*Thylogale brunii* (Schreber, 1778)

Fig. 4a Lateral view of left juvenile premaxilla and maxilla, AM F54760.

Fig. 4b Stereopair of occlusal view of AM F54760.

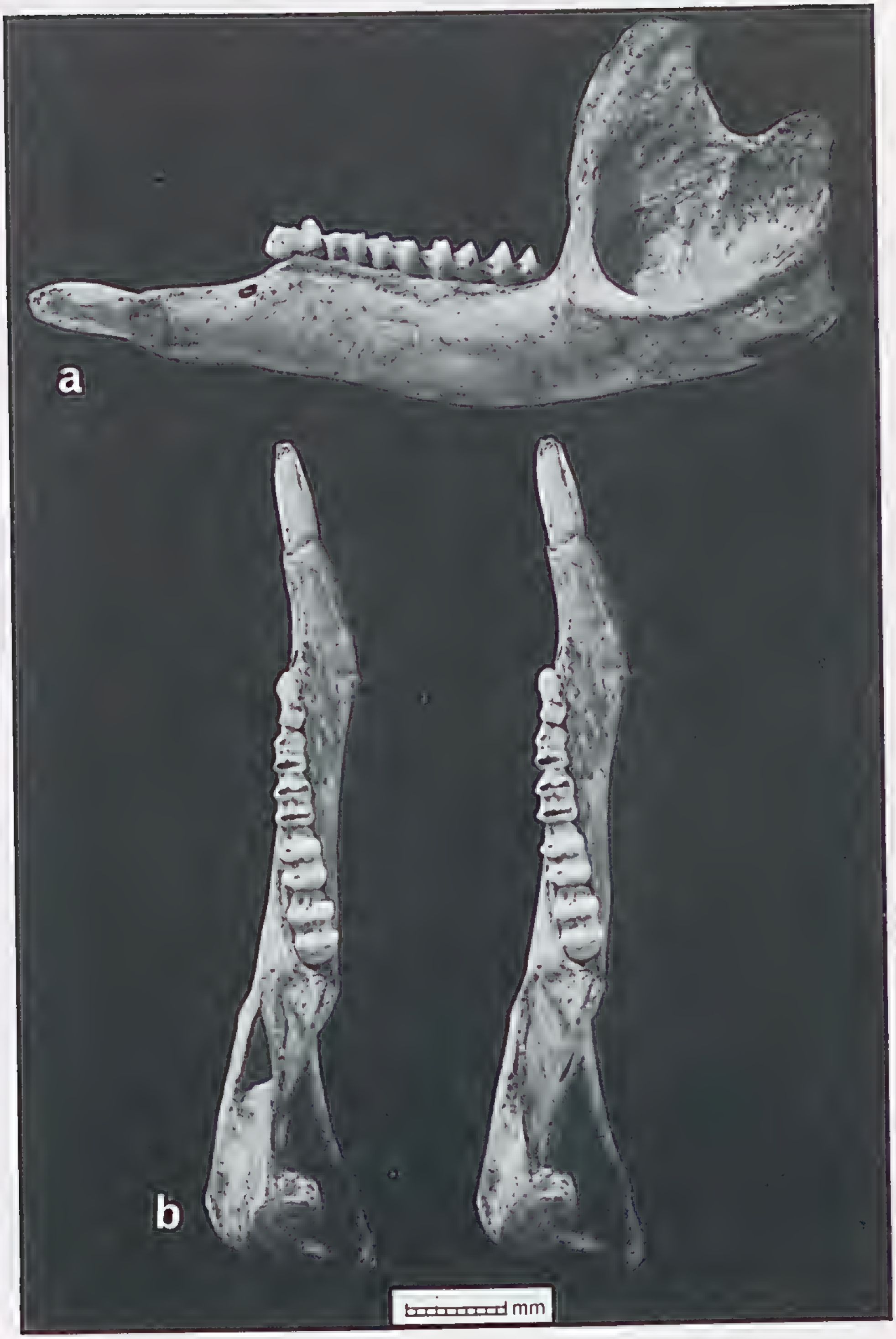

Fig. 5

*Thylogale brunii* (Schreber, 1778)

Fig. 5a Lateral view of left adult mandibular ramus, AM F54762.

Fig. 5b Stereopair of occlusal view of AM F54762.

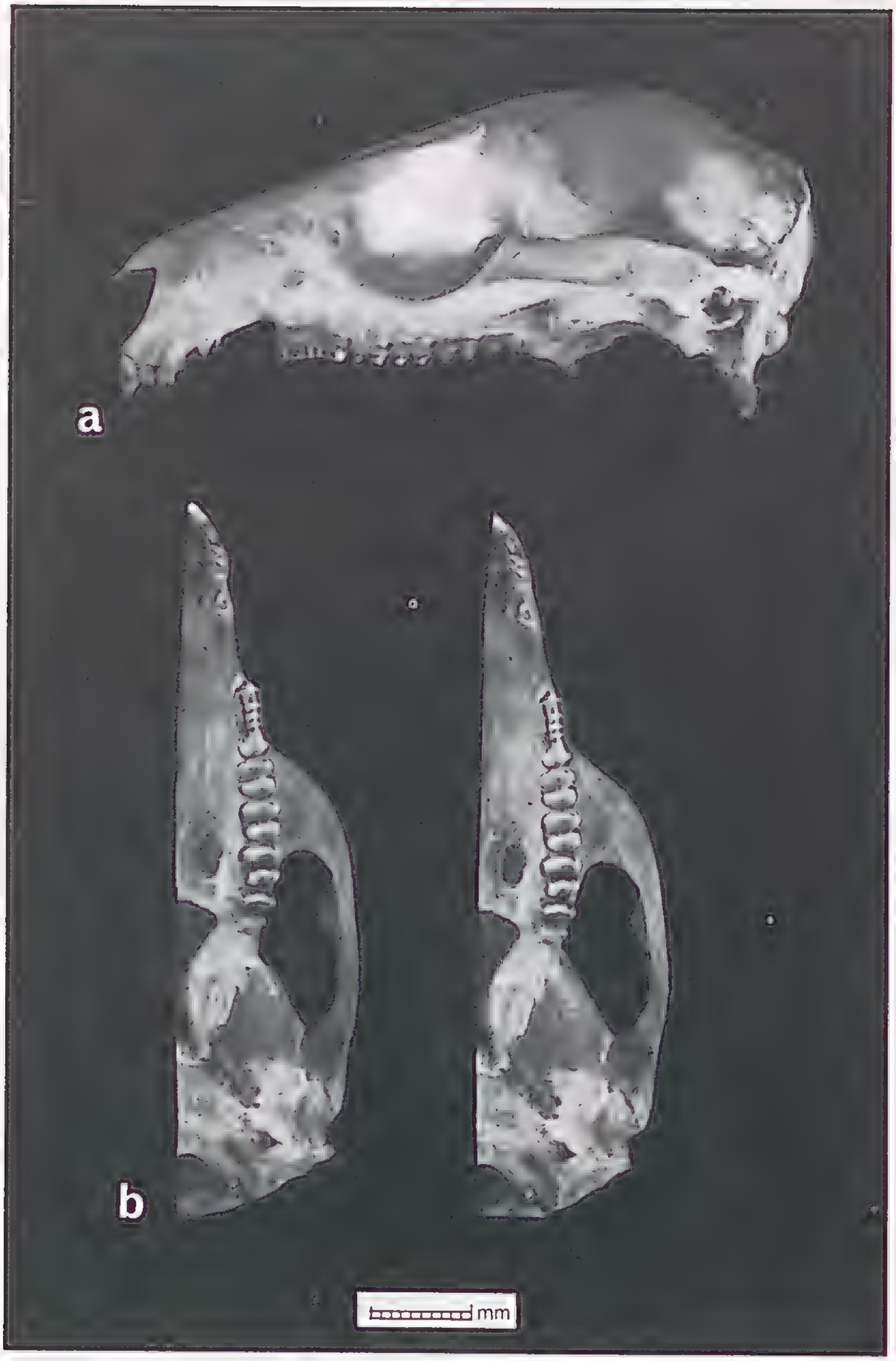

Fig. 6

*Dorcopsulus vanheurni* Thomas, 1922

Fig. 6a Lateral view of adult skull, CM 15124.

Fig. 6b Stereopair of occlusal view of left side of skull, CM 15124.

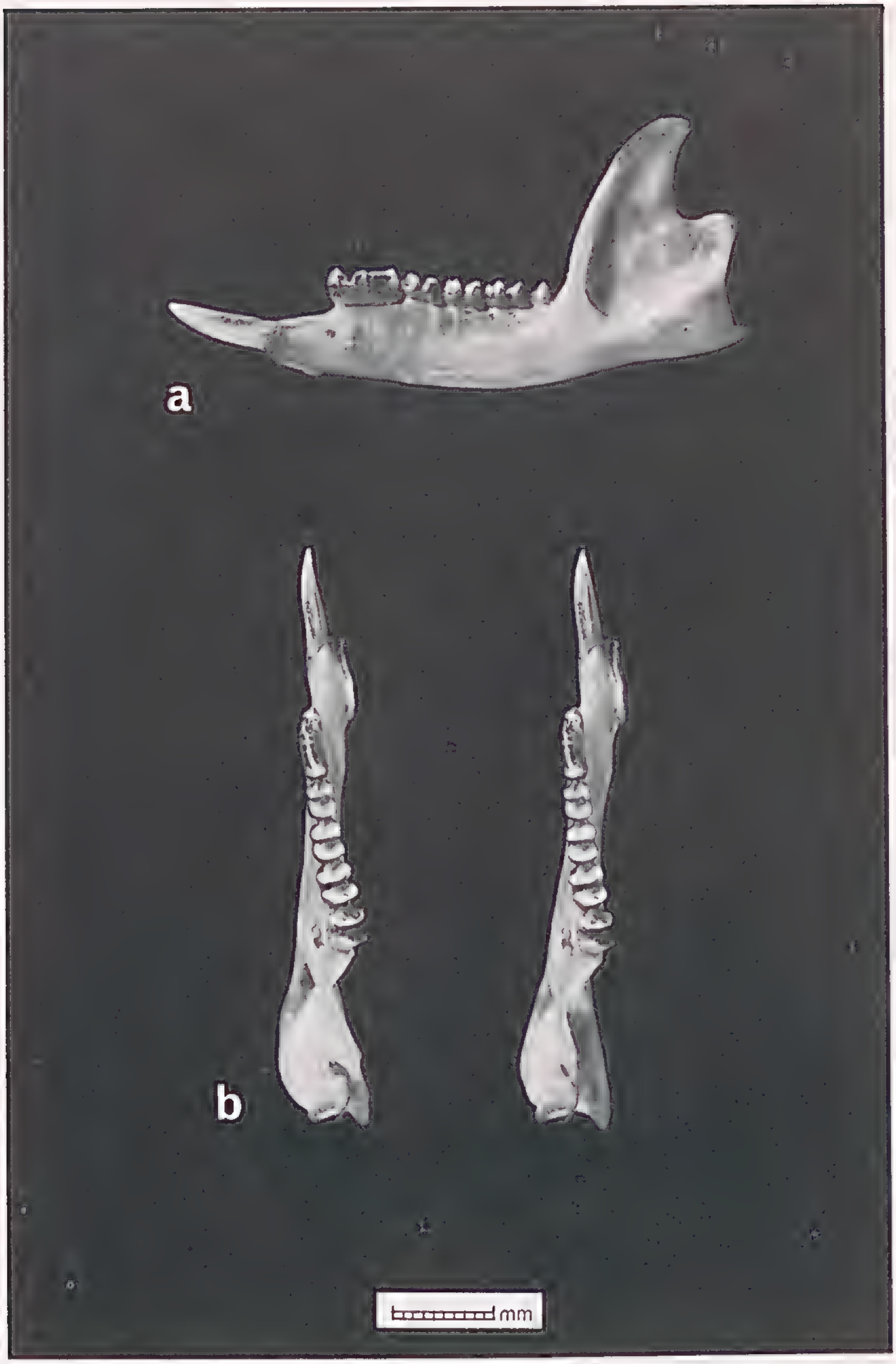

Fig. 7

*Dorcopsulus vanheurni* Thomas, 1922

Fig. 7a Lateral view of left adult mandibular ramus, CM 15124.

Fig. 7b Stereopair of occlusal view of CM 15124.

# RESULTS OF AN ARCHAEOLOGICAL SURVEY OF THE HUNTER RIVER VALLEY, NEW SOUTH WALES, AUSTRALIA

## Part II: Problems of the lower Hunter and contacts with the Hawkesbury Valley

DAVID R. MOORE

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## INTRODUCTION

The first part of this report, published in 1970, described the survey and excavations carried out in the upper Hunter Valley from its source down to the Singleton area and in the Goulburn Valley from its rising on the watershed of the Divide down to its junction with the Hunter near Denman. The sites selected for excavation were all found to be Bondaian throughout (i.e. backed blades and microliths predominated). The valley sites were dated to around 2000 BP, whereas the one site excavated outside the valley on the Divide, near the headwaters of the Goulburn, appeared to date from about 7750 BP. (But see note at end of introduction.) At this stage, the number of occupation sites investigated was not sufficient to form any conclusions.

On completion of this section of the project at the end of 1967, the intention was to continue the survey downstream to Maitland and the Hunter estuary, in order to provide material for a comparison between Aboriginal exploitation of the freshwater and tidal zones of the river system. However, after extensive reconnaissance, it became clear that any occupation sites on the lower Hunter likely to contain *in situ* remains had been obliterated or destroyed by the intensive European use of the region.

As was described in the historical introduction to Part I of this report, the timber of the lower Hunter was progressively stripped from 1802 onwards and subsequently the fertile alluvial flats were extensively modified for agriculture and grazing. In addition, the valley periodically suffered devastating flooding. Around Newcastle itself vast areas of estuarine shell middens were removed and burnt for lime to make mortar. From the start of settlement in 1801 the progressive exploitation of coal seams also brought about substantial modification of the landscape. A particularly drastic change was the removal of cover upstream from the Hunter-Paterson junction by cedar-getters during the 1830s and 1840s. The early surveyors, such as Henry Dangar, reported impenetrable scrub and rainforest on both sides of the river for several miles (see Wood, 1972: 2-3) and this may well have formed an effective barrier to communication between the Aborigines of the lower and middle Hunter in prehistoric times. It is also possible that this was a survival of a

Records of The Australian Museum, 1981, **Vol. 33 No. 9,** 388-442, Figures 1-15.

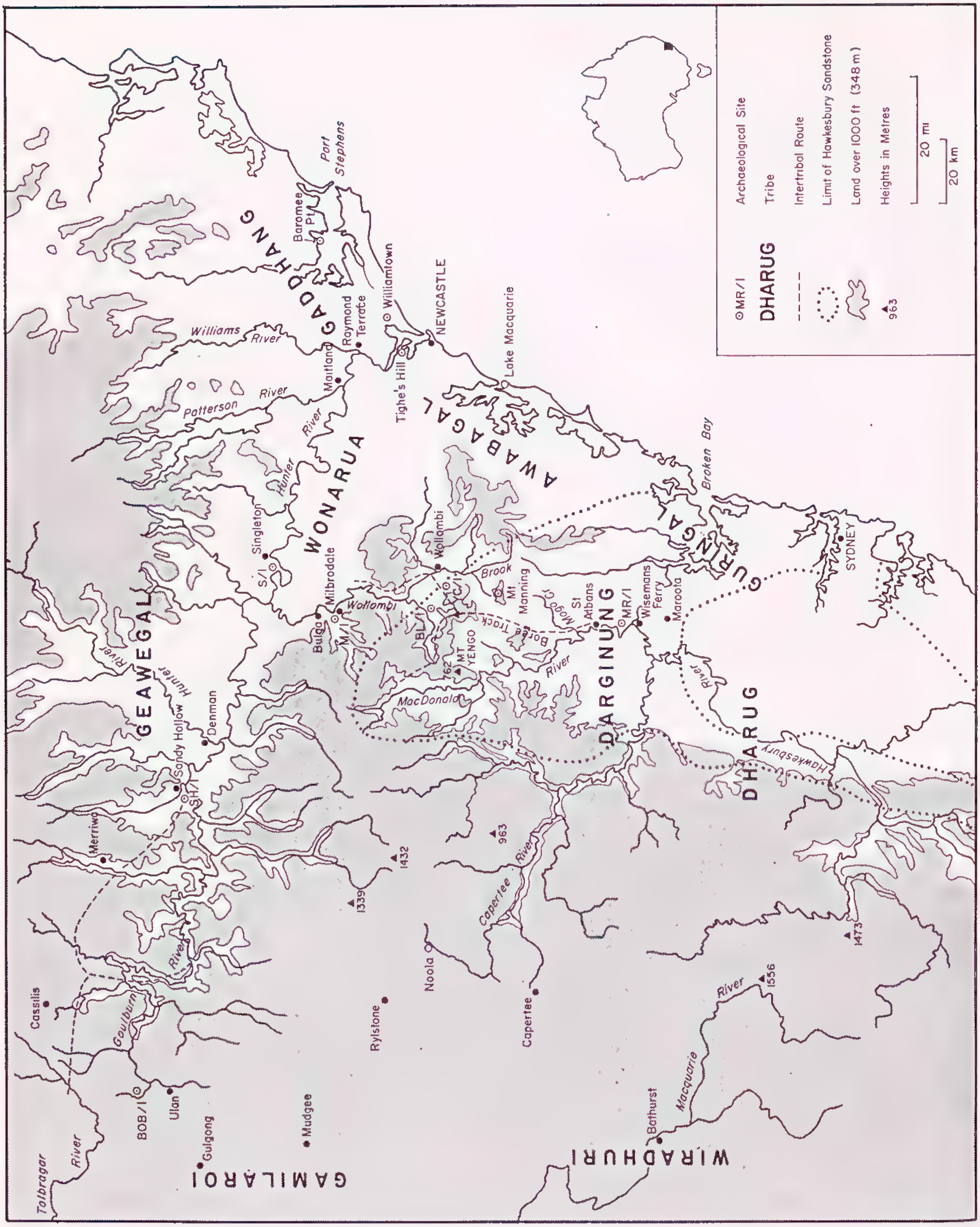

Fig. 1. Archaeological Map: Hunter and Hawkesbury River Systems

much more extensive rainforest system which had gradually contracted as a result of decreasing rainfall after the cessation of the last glacial. However, it is unlikely that rainforest could ever have existed except on the rich alluvial flats of the lower Hunter.

At the time of the commencement of this survey some remnants of the formerly huge shell heaps on the swampy islands in the Hunter estuary still remained (see Fig. 5), but before it was possible to investigate them in any detail they were bulldozed out of existence for road-fill and factory development. Attention was therefore turned to the valleys of the Paterson and Williams Rivers, which feed from the north into the lower estuary of the Hunter, but here also modification by agriculture and flooding had obliterated all signs of the previous Aboriginal occupants. The few caves and rock shelters in the area showed no signs of occupation deposits, nor was any rock art encountered.

Along the coastline north and south of the Hunter entrance innumerable remains of shell middens can still be seen, but these almost invariably amount to no more than random scatters of shells on shifting dune systems which after storms produce flakes and implements in large numbers. These scatters have been picked over by collectors for many years and some of these collections are deposited in museums, as will be described in the next section.

Since the lower Hunter area seemed unlikely to provide any sites suitable for excavation, the survey was next extended up the coastline north of the Hunter entrance and eventually included Port Stephens. According to Enright (1932) and earlier observers, such as Dawson (1830) and Threlkeld (1824-59), the Gaddhang (or Worimi) people occupied the northern bank of the Hunter estuary and their territory extended as far north as Port Stephens. So it was felt that a stratified site, if such could be found, even as far afield as the northern shores of Port Stephens could provide useful evidence to compare with the upper Hunter sites. After extensive reconnaissance, it was decided to test a consolidated midden on a rocky headland at Baromee Point (Port Stephens, 1-63360, ref. 063605). Although there are remains of open middens at many points around Port Stephens (for example at Tahlee, Mulwee, and North Arm Cove), they appear to have been interfered with and modified, either by collectors or for use as road fill, whereas the Baromee Point site was covered with grass and unlikely to have been affected by European activity. One test square was dug in the centre of this site, during January 1968. The excavation went through five 6-inch levels to 30 inches, where tumbled rock and heavy clay were reached. Apart from much fragmented shell and some bone fragments, the test square produced little except large natural chunks of the local conglomerate rock. These might have been used for knocking shellfish off rocks, but there were no definitely identifiable implements in any level. Nor was there any indication whatsoever of stratification.

As a result of the inconclusive outcome of all these reconnaissances, it was decided to divert the survey to the area between the middle Hunter and the Hawkesbury Valley to the south, along the line of the Wollombi Valley, Mogo Creek, and the lower Macdonald Valley. This area is rich in both rock engravings and cave paintings and is documented (see Sim 1966) as having been a traditional route along which the Darginung of the Hawkesbury made contact with the Wonarua of the central Hunter region. This survey was commenced in 1969 in the Wollombi area and many art sites and rock shelters were inspected. Most of these had suffered interference and vandalism, but two sites selected for testing were apparently intact. One was a painted shelter high in the hills on Stockyard Creek, west of Wollombi, the other, a large overhang without paintings, was on a creek near the Mount Yango road, south-west of Wollombi. These test excavations were completed in 1970 and both the material obtained and the results of radiocarbon dating closely paralleled the Hunter sites previously investigated.

Reconnaissance in the rugged country southward to St Albans revealed much rock art but an almost total absence of occupation sites. One painted shelter at Mount Manning had already been excavated and published by Macintosh (1965), the deposits being apparently no more than a few hundred years old. Others who had worked over the area recording rock art (notably I. M. Sim, pers. comm.) confirmed that occupation sites were extremely rare, so attention was concentrated on the lower Macdonald Valley, between St Albans and Wisemans Ferry.

Eventually a large shelter containing very faded paintings, on the southern side of the river, was selected for excavation. A test square excavated in 1972 indicated that the site was a promising one and charcoal processed at Sydney University indicated an antiquity of at least 6000 BP for the start of occupation. Due to the author's commitments to fieldwork in the Cape York region during the next few seasons, it was not possible to follow up this promising lead until 1976-77, when full excavation of a transect from back wall to talus slope was completed. Although the yield of implements was scantier than in the Hunter sites, it was clear that the deposit was Bondaian throughout and a much wider variety of materials had been used, including some undoubted Hunter Valley cherts. Study of the sources of these materials seemed likely to provide evidence for trade, both northward and southward, so this was undertaken under the supervision of Professor D. Branagan of the University of Sydney. At the same time a computer programme was commenced by David Hain, of the C.S.I.R.O. Computing Research Centre, to see whether any significant information could be obtained from a statistical comparison of samples of Bondi points from all of the excavated sites. Samples from surface collections from sites north and south of Newcastle were also included. The intention of this project was to ascertain whether any differences in technique and material could be detected, both synchronically and diachronically, as well as spatially.

The remainder of this report will consider the problems of the Hunter estuary in more detail, then describe the Wollombi and Macdonald River excavations, and finally the results of materials analysis and computer comparisons will be outlined, in order to draw conclusions from the total results of the survey.

As in the first part of this report, all basic data obtained from the excavations will be given in full, to enable other research workers to make comparisons with their own findings. All of the actual material from these excavations, together with sundry surface finds, is in the archaeological collections in the Australian Museum and can be made available for future study. In addition, data from all field reconnaissances made by the author have been incorporated into the central records of Aboriginal sites maintained by the N.S.W. National Parks and Wildlife Service.

### Note on dating of Site BOB/1

Subsequent to the publication of Part I of this report, further charcoal samples from site BOB/1 were processed. The original date for charcoal from 25″-30″ at this site, on Bobadeen property, near Ulan, seemed too early for the Bondaian material with which it appeared to be associated (ANU-124: 7750 ± 120 BP), so a further sampling was made. Charcoal from 25″-26″ was dated to 5150 ± 170 BP (ANU-287) and from 21″-23″ to 4120 ± 175 BP (ANU-790). The consistency of these dates seems to indicate that occupation at BOB/1 began at about 6000 BP. Possibly the few artifacts associated with ANU-124 had been trodden down into pre-occupation deposits containing charcoal from bushfires.

## PROBLEMS OF THE HUNTER ESTUARY

Judging by the sparse early accounts of Aboriginal life on the Hunter estuary (e.g. Paterson, 1801, Barrellier, 1802, Dawson, 1830, Threlkeld, 1824-59), it is likely that the people spent a large proportion of their time on the river, poling themselves around in their bark canoes and either catching fish with line and spear or landing to collect shellfish and plant foods. So far as shell foods are concerned, some idea of the range collected and eaten in the estuary may be indicated by a sampling made on 12/3/70. This sample was collected independently by the author and another archaeologist, Dr S. M. Bard, from the bulldozed section of the last remaining shell heap on Ash Island (Newcastle 1-63360, ref. 750360). This section may be seen in Fig. 5. When the two samples were compared, the principal food shells represented appeared to be as follows (The assignment of percentages is subjective, derived from the visual appearance of the section):

| | |
|---|---|
| _Ostrea angasi_ (Sowerby) — "mud oyster" | c.40% |
| _Anadara trapezia_ (Lamarck) — "Sydney cockle" | c.30% |
| _Soccostrea commercialis_ (Iredale & Roughley) — "rock oyster" | c.10% |
| *_Chlamys lividus_ (Lamarck) — "Tasmanian scollop" | c.10% |

Shells represented in lesser quantities were:

_Notospisula trigonella_ (Lamarck)
_Trichomya hirsuta_ (Lamarck) — "estuarine mussel"
_Velacumantus australis_ (Quoy & Gaimard) — "whelk"
_Septa (Monoplex) parthenopea_ (v. Salis)
_Circe sugillata_ (Reeve)
_Conuber conica_ (Lamarck)
_Conuber sordidus_ (Swainson)
_Neosolen correctus_ (Iredale)

These identifications were made by Dr W. F. Ponder of the Australian Museum.

Special mention is made in early reports of the considerable dependence of the estuary Aborigines on "fern roots", by which presumably the common bracken fern _(Pteridium esculentum)_ is meant, but probably bulbs and succulent roots of swamp and marsh plants were also included. Before European settlement the estuary was fringed with mangroves, behind which, especially on the left or southern bank, existed extensive marshes where not only innumerable waterbirds could be easily caught but also an abundance of water-lily and other roots were available. The Hexham Swamp, a basin about eight kilometres in diameter ringed with low hills, has been almost completely drained and turned into grazing land. Search of the surrounding hills failed to reveal any clue as to location of Aboriginal campsites, but there, too, European settlement had brought about extensive modification long before the end of the nineteenth century and now the whole area is covered with pasture.

Nearer the Hunter mouth on the southern side was another extensive swamp and floodplain, traversed by tidal creeks and protected on the seaward side by Nobby's Head and Shepherds Hill. This area was separated from the Hexham Swamp by an isolated elevation of the Tomago coal measures, capped with sandstone. On this slight ridge are now situated the inner suburban developments of Mayfield, Tirrikiba and Tighe's Hill. In pre-European times this ridge would have formed the only dry land in the whole swamp area and would obviously have been a favoured campsite. It is significant that all three of these suburbs have in the past been prolific collecting grounds for Aboriginal stone implements. One such collection was made during the first quarter of this century by D. F. Cooksey of Mayfield and presented to the British Museum in 1927. This collection contains representative artifacts from each of these localities, including Bondi points, large split pebble slices and massive core choppers. The latter two categories are not

*It has been suggested by Professor L. K. Dyall of the University of Newcastle that this and other huge shell heaps on the islands of the Hunter estuary may not, in fact, have been Aboriginal middens but rather the result of European dredging, which commenced early in the life of the settlement. Certainly it is difficult to see how the Aborigines could have obtained _Chlamys lividus_ in the Newcastle area. Artifacts were present in these heaps, but were rare. These could, of course, also have been dredged up from the river bed.

represented in the upper and middle Hunter sites excavated. The author was able to examine and photograph this collection in 1969 (see Fig. 6). Some remnants were presented to the Australian Museum by the collector's son in 1929 and contain the same range of implements.

The presentation to the Australian Museum of a collection made on one site at Tighe's Hill during 1964-66 by A. J. Gwynne of Lambton first drew the author's attention to this area and in 1969 he was shown the actual find spot by Mr Gwynne (ref. Newcastle 1-63360—775323). The material had all eroded from the east side of Tighe's Hill due to the bulldozing of a flat for a factory site. The top of the hill had obviously been an important Aboriginal camping place, but the whole area of Tighe's Hill was intensively built over as a suburban development during the late nineteenth and early twentieth centuries. In fact, the houses and yards are constructed on top of what appears to be an extensive stratified midden and it was from one edge of this that the Gwynne collection was obtained. It is not now possible to excavate anywhere in the area, but should further development occur, salvage excavations should certainly be carried out, since this is probably the last remaining place where a datable sequence for the lower Hunter can still be found.

The Gwynne collection is an important one, because it represents a careful gathering over several years of all implements and waste flakes eroding from one particular part of this site and may be treated as a random sampling reasonably representative of the total site. In addition to Bondi points, massive flaked slices and core choppers similar to those in the Cooksey collection are well represented. There are also very large backed blades, like giant eloueras (see Fig. 7). The majority of these implements are made from the pale grey to white chert obtained from the outcrops to the south of the Hunter entrance, designated geologically as Mereweather chert but known popularly as "Nobby's chert" after the headland of that name; pink quartzite and black chert are also present in small quantities. The Gwynne collection contains a total of 419 artifacts and a count of the basic types represented gave the following proportions:

| **Implement Types** | **Range (max. dimension) (centimetres)** | **Percentage of total sample** |
|---|---|---|
| Cores ("horsehoof", "turtleback", and other) | 2.5-10 | 6% |
| large flake slices ("worimi cleavers") | >10 | 2% |
| Truncated blades ("choppers", "adzes") | 2.5-12.5 | 4% |
| Large unmodified blades | 5-7.5 | 11% |
| Short blades ("side scrapers") | 2-5 | 14% |
| Short pointed blades ("knives") | 2-5 | 14% |
| Backed blades ("Bondi points") | 2-5 | 2% |
| Narrow flakes ("points", "end scrapers") | 2-7.5 | 8% |
| Broad flakes ("scrapers") | 1-6.5 | 33% |
| Utilised pebbles | | 1% |
| Miscellaneous flakes | | 4% |

In addition there was one nosed blade ("drill") and one edge-ground axehead of coarse tuff. It is noticeable that the large core and flake component is very heavily patinated to a dark brown colour, though the basic material is preponderantly white-grey chert, whereas the small-tool component shows little discolouration. Examples of the main tool types present in this collection are illustrated in Fig. 7.

More recently, from 1965 on, Dr (now Professor) L. K. Dyall of the University of Newcastle carried out a long-term project to systematically collect over erosion and sand-dune sites in an area extending from Port Stephens in the north to Lake Macquarie in the south. In many cases his sites coincide with those previously collected by Cooksey. Dyall's collections, with excellent documentation, have been progressively deposited in the Australian Museum and he has published two papers summarising his findings in *Hunter Natural History* (Dyall, 1971, 1972). Although his categorisation of types does not exactly coincide with that used here, a breakdown of his figures for collections from near Williamtown, to the north of the Hunter mouth, and from the Swansea area, at the mouth of Lake Macquarie, show percentages similar in the main to those given above for the Gwynne collection:

*Williamtown site. N = 1717*

| | |
|---|---|
| Cleavers | 0.3% |
| Knives | 9.8% |
| Scrapers | 36.7% |
| Bondis | 14.1% |
| Geometrics | 23.5% |
| Cores | 11.7% |
| Pebble tools | 0.9% |
| Miscellaneous | 3.0% |

*Swansea Heads site. N = 500*

| | |
|---|---|
| Cleavers | 5% |
| Knives | 10% |
| Scrapers | 25% |
| Bondis | 3% |
| Cores | 10% |
| Pebble tools | 27% |
| Miscellaneous | 20% |

Bondi points from these two sites have been included in the computer analysis of backed blades from all the sites excavated during this survey, to provide a comparison with the coastal and estuarine region.

Although backed blades and microliths appear in considerable quantities in most of these estuarine and coastal sites, there is usually the further component of large flake and core implements not present in the excavated middle and upper Hunter sites. It may possibly be connected with shell-gathering activities, or perhaps with the chopping down and preparation of mangrove timber, which must have been widely used for poles, paddles, canoe stretchers, and all situations where toughness and resilience to water action were required. Alternatively, it may represent the earlier large core and flake tool tradition identified elsewhere in the continent as preceding the microlithic or small-tool industry. The marked patination of the Tighe's Hill large tools might be taken to support the latter supposition. It is also significant that whereas this large tool component was completely absent from the upper Hunter excavated sites, it was present in the surface collections made by McCarthy and Davidson (1943) on the Gowrie terrace and at Bulga, west of Singleton. This would imply that the large core and flake tool tradition preceded the small-tool industry on the freshwater reaches of the Hunter and it is likely that this would also have been the situation in the estuarine section. It is, however, possible that the large tools continued to be made in the estuary and on the coast for specialised uses, such as those suggested above. In the absence of a stratified and dated sequence for the Newcastle district, it is impossible to be certain which of these options is correct.

So far as the wooden implements and weapons of the lower Hunter people are concerned, we are fortunate to have two sets of illustrations, drawn directly from actual objects. The first of these is in the Scottowe manuscript in the Mitchell Library and is reproduced in Gunson (1974:81). This was drawn by the convict artist, R. Browne, presumably in about 1813, since this is the date of the manuscript notes accompanying the illustrations. Included are four types of spears: a four-pronged fish spear, plain and single-barbed hunting spears, and a fighting spear with three wooden barbs cut in. An elliptical shield is decorated with a double grooved St George's cross and a single grooved St Andrew's cross. The spearthrower is the typical east coast spatulate type, with cut-in wood peg. Two clubs are shown: one has a thin handle, swelling slightly towards the further end, which is pointed, the other has a disc-shaped head narrowing to a point. The axe illustrated appears to have a European iron blade, but is hafted in the traditional fashion, with a sapling or strip of cane passed around the head. The boomerang is pointed at both ends and slightly elongated at the held end. Also shown are a palmleaf basket with handle, a water-carrier made of a hollowed tree-gnarl, a twined dilly bag, and a fishing line with shell hook. The other illustration was published by B. McKiernan in *Anthropos* in 1911 and was drawn from a small collection unearthed in good condition during the digging of a drainage ditch near Raymond Terrace. It shows a prong from a multi-pronged fish spear (two were in fact found), a shield somewhat different from that in the Browne sketch, since it has incised wavy lines running along its whole length and two recesses on the edges at the middle, presumably for binding on a handle. A spearthrower is also illustrated, of the spatulate type, but in this case the peg is attached with gum.

If one adds the pounding stones for roots and nuts, the stout digging sticks, and various types of coolamons mentioned in early accounts as used by the women, then the essential maintenance and extractive gear of the region is almost complete. Bark canoes and huts, together with sewn skin cloaks and blankets were additional basic equipment. We do not have any information on the implements used in this region for the very essential function of fire-making.

On checking over this list, it is immediately apparent that remarkably few components are likely to survive in an archaeological context. Edge-ground axe heads, stone pounders, and possibly shell fish hooks might be expected to endure, and bone spear points and barbs appear occasionally in specific horizons. However, none of the accounts of the Aboriginal toolkit in the Hunter region supply any explanation for the profusion of backed blades and microliths which have been collected over the years on innumerable coastal and estuarine sites. Nor do they definitely identify the large core and flake component as having been in use in the historical period.

At this stage, this is as far as one can go in evaluating the tools, weapons, and ecology of the Hunter estuary. For this reason, the survey was diverted to the Wollombi-St Albans axis, as was explained in the introduction. The next (and main) part of this report is therefore devoted to the field reconnaissance and excavations carried out during 1969-77.

## CONTACTS BETWEEN THE HUNTER AND HAWKESBURY VALLEYS

As previously mentioned, there are many occupation deposits in rock shelters in the area drained by Wollombi Brook (a southern tributary of the Hunter), whereas in the rugged and mostly dry watershed between the headwaters of Wollombi Brook and the Valley of the Macdonald (which enters the Hawkesbury near Wiseman's Ferry) rock shelters are rare and occupation sites even rarer. However there are in this area some other potential sources of information not present in the Hunter estuary, for it is one of the richest rock-art regions in the whole of eastern New South Wales. This art has been discussed by Sim (1965), McCarthy (1956, 1959, 1961, 1965), Maynard (1965), and others and it is not intended in this context to cover the same ground again. However, certain observations may well have an important bearing on the archaeological situation and, in fact, it was largely due to these considerations that the survey was extended into the Wollombi-St Albans area.

Firstly, then, the rock engravings of the Sydney region are confined strictly to the Hawkesbury sandstone area, that is from the Bulli escarpment in the south to the southern watershed of the Hunter in the north. The actual northern limit may be seen on the archaeological map at the beginning of this part of the report (Fig. 1). The style of the rock engravings throughout the Sydney-Hawkesbury region is homogeneous, although there are considerable variations in motifs in the differing ecological zones. In the area between Wollombi and St Albans, as well as a number of outstanding engraving sites, there are also some painted rock shelters, and the paintings in these seem to conform in general to the Sydney style which is characterised by comparatively realistic representations of people and animals, either totally infilled or else in charcoal or ochre outline, groups or lines of small human figures dancing and carrying out other activities, and various types of stencils. Certain connexions, in both style and motif, with the rock engravings of the same area can be detected (see Maynard, 1965).

Secondly, in the area immediately to the north of the Hawkesbury sandstone, particularly around Wollombi, Broke, Milbrodale, and Bulga, there are innumerable painted caves which have many features in common but which differ considerably from the cave paintings to the south. In this area there is an extensive use of stencils of hands, sometimes including the whole arm, of weapons and tools such as boomerangs, spearthrowers, axes, etc., and occasionally stencils of minature human figures. Also common are series of straight white lines ("tally marks") and radiate figures in white ("sun symbols"). Representations of animals are extremely rare. Some shelters contain what seem to be meaningless masses of stencils with indiscriminate superimposition; in others they seem to be carefully placed in some significant relation to one another. The problems concerning the use of stencils in this area have been discussed in the author's paper given during the symposium on "Schematisation in Art" at the Australian Institute of Aboriginal Studies General Meeting in Canberra in 1974, subsequently published under the editorship of P. J. Ucko (1977), and need not be repeated here.

R. H. Mathews (1897a) obtained definite information from Darginung remnants at Windsor in 1895 that the traditional Darginung territory extended from the Hawkesbury to near Wollombi, so it is a reasonable assumption that the northern limit of the engravings coincides with the junction of the Darginung and Wonarua territories. This would mean that all the cave paintings on the southern fringes of the Hunter Valley, including Milbrodale and the Wollombi Valley, are the products of the Wonarua or their ancestors, whereas both paintings and engravings south of Wollombi as far as the Hawkesbury were part of the Darginung culture. Nevertheless, both areas would undoubtedly have been visited by both groups at different times, for ceremonies and trade exchanges, such as are frequently referred to in the early accounts. Incidentally, Mathews, in the same article, states that some of the old Darginung men had seen both rock engraving and painting carried out by members of their tribe in about 1843-1855.

However, one site in Wonarua territory does not seem to fit the tribal art pattern suggested above. This is the well-known open shelter at Milbrodale, adjacent to excavation site M/1 and already mentioned in the first part of this report. The interpretation of this site is discussed in the author's paper referred to above (in Ucko, 1977), but it is the stylistic relevance of these remarkable paintings that has more point here. They comprise one large red human figure with very elongated outspread arms and a number of widely spaced stencils of hands, arms, and implements, including boomerangs, axes, and a spearthrower (see Fig. 15). These appear to have been very carefully placed in order to tell a definite story related to the giant human figure. This site is totally unlike any other in the whole Hunter Valley and is also possibly of greater antiquity than any other, since it was so old at the time of first settlement in the vicinity that the local Aborigines knew nothing about it (or, at least, this was what they stated. See Mathews, 1893). The only art in the whole Sydney-Hawkesbury region with which it appears to have any affinity is another well-known painted site at Maroota, just south of Wiseman's Ferry, reported on by McCarthy (1961). This shelter also contains a large human figure, with a bird-like head, which extends from floor to roof and even overhead onto the roof itself. This site also has carefully placed stencils and in addition, a long and sinuous snakelike figure extending back and forth across the back wall. The application of ochre in the main figures is also similar at both sites, it having apparently been applied by rubbing hard along the surface, as if with a greasy crayon. This has left nodules of colour on all small projecting parts of the rock and has also forced the ochre well into the surface. The technique is unusual and it may be responsible for the remarkable state of preservation of both sites. (It should be added that McCarthy's identifications and interpretations differ somewhat from those given here.)

All of this leads to the possibility that the Milbrodale paintings may have been done by people either from the Hawkesbury or at least well-acquainted with the art of the Hawkesbury area. It is possible that the groups encountered historically on the Hunter were comparatively recent arrivals and that the southern fringes of the valley had previously been included in the territory of the Hawkesbury Valley people. Similarly, the frequent incursions of the Gamilaroi from the west of the Divide into the Goulburn and upper Hunter may be related to a late occupation by the Wonarua and Geawegal. This would accord with the lateness of the dates from occupation sites in the valley itself, as compared with sites excavated immediately outside the Hunter and Goulburn Valleys, which appear to have been occupied three or four millenia earlier. These suggestions will be further considered in the Discussion which concludes this report.

Having established the art context of the area under discussion it is appropriate to continue the report of the archaeological survey and to describe the excavations carried out in Wonarua and Darginung territory.

### The Wollombi Excavations

The country around Wollombi is both rugged and close, being well covered with sclerophyll forest and scrub, apart from where the broader valleys have been cleared for grazing. There are a great many rock shelters, both in the valley sides and in the mountains, and a high proportion of them contain paintings. Many also show signs of Aboriginal occupation, but in most cases the deposits are merely superficial or have obviously been dug through by collectors. It is not therefore easy to find sites with any likely archaeological potential.

**Big L** (Map: Cessnock, 1 to 63360). See Fig. 8.

The first site tested was reported by L. K. Dyall, who in 1968 excavated a trial trench, with the assistance of R. W. Northey of Wallsend. This trial seemed to indicate a stratified sequence of considerable age, so an inspection of the area was carried out by an Australian Museum party in April 1969. The shelter stands on a hillside, due west of Wollombi, about 200 yards above Big L Creek, which is an arm of Upper Stockyard Creek (ref. 031253). It contains paintings and stencils in a good state of preservation (see Fig. 9) and its situation is of particular interest, since it is at the extreme northern edge of the Hawkesbury sandstone. On a high ridge about one mile south of the shelter is the most northerly group of rock engravings, known as the Finchley's Trig group (ref. 014236).

The owner of the property in which the rock shelter is located, Mr G. Cooper of Wollombi, had used it as a camping place when rounding up cattle in the hills and had installed a wooden table and bed in it, but this had not interfered with the deposits to any extent. Mr Cooper readily gave permission for the excavation to be carried out.

In August-September 1970, a small party tested the site, which was code-named BL/1. A grid was laid out on a datum line with a bearing of 142°, well clear of Dyall's trial trench and in the approximate centre of the deposit. For reasons which will become apparent later, one three-foot square only was excavated across the dripline in three-inch levels. Sieving was through ⅛ inch mesh.

After the first two levels, which were composed of fairly soft loam, compacted yellow grit was reached, with frequent chunks of sandstone. Implement yield then steadily increased, Bondi points, eloueras, geometrics, and fabricators being represented. Fair quantities of charcoal and some extremely fragmented bone were also present. In level 5 an apparent fireplace was encountered in the southern half of the square. Level 7 was particularly productive, with a new component of scrapers and adze flakes of black siliceous material. Rock chunks increased in levels 9 and 10, while implements lessened and in level 11, at 38 inches, rock slabs, interspersed with yellow sterile sand, were reached.

Distribution of implements and waste by levels is shown in Tables 1-2. Charcoal from level 9 was subsequently radiocarbon dated to 480 ± 75 BP (ANU-648). This is a remarkably recent date, when compared with other sites to the north with similar depths of deposit, but there was no reason to suspect contamination or other interference, so it was decided that it would not be profitable to continue the excavation. The survey was therefore extended to endeavour to find a more significant site. In 1977, in order to check this anomalous date, charcoal from level 8 was submitted to the Sydney University Radiocarbon Dating Laboratory and returned a date of 2495 ± 105 BP (SUA-756). This seems more likely to be correct when it is compared with the other Hunter dates, but the reason for the unconformity between the ANU and SUA dates for BL/1 remains unexplained.*

**Yango Creek** (Map: Cessnock, 1-63360). See Fig. 10.

After extensive reconnaissance, a promising site was found in a large unpainted overhang near Yango Creek, south-west of Wollombi (ref. 118224). The roof of this shelter is about 30 ft. high and the overhang is about 100 ft. long and 20 ft. deep. The deposit has formed over the outer half of a rock floor which slopes at about 20° and extends outside the dripline. A large wombat burrow in the centre of the deposit showed artifacts in the spoil and walls, together with shells of freshwater mussel. Subsequently

*In a letter dated 1/2/78, Mr Henry Polach has explained that in March 1973, due to anomalies in datings of certain samples run during an equipment change in 1972, ANU-648 was rerun and gave a date of 920 ± 75 BP (ANU-648/1). Part of the same sample was then again run, on a three-day count, and returned 930 ± 50 BP (ANU-648/2). Nevertheless, the reversal between ANU-648 and SUA-756 still stands and is impossible to explain. Archaeologically SUA-756 seems more likely.

## TABLE 1. SITE BL/1: DISTRIBUTION OF STONE IMPLEMENTS AND WASTE

| | Square | A | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Level | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | Total |
| Blade, backed | Bondi | 2 | 4 | | 2 | 1 | 9 | 23 | 9 | | 1 | | 51 |
| | Elouera | 1 | 3 | 1 | 3 | | | 1 | 1 | | | | 10 |
| | Microlith | 1 | | | 3 | 6 | 8 | 9 | 3 | 3 | | | 33 |
| | Other | | | | | | | | 1 | 1 | | | 2 |
| Scraper | Side | 6 | 7 | 1 | 9 | 3 | 5 | 5 | 7 | 3 | | | 46 |
| | End | 2 | | | | 2 | | 1 | | | | | 5 |
| Point, worked | Uniface | 2 | | | 1 | 4 | 1 | | | 1 | | 3 | 12 |
| | Other | 4 | 2 | | 3 | 5 | 15 | 14 | 10 | 3 | | | 56 |
| Flake, utilized | Blade | | | | | | | | | | | | |
| | Other | | | | | 2 | | | | | | | 2 |
| | Adze flake | 3 | 2 | 1 | 4 | 3 | 5 | 7 | 2 | 4 | | | 31 |
| | Fabricator | 5 | 2 | 2 | 9 | 5 | 6 | | 4 | | | | 33 |
| | Core, utilized | | | | | 3 | 4 | 1 | | | 1 | | 9 |
| | Axe, gr. edge | | | | | | | | | | | | |
| | Pebble, utilized | | | | | | | | | | | | |
| | Misc. | | | | | | | | | | | | |
| Sub Totals | Implements | 26 | 20 | 5 | 34 | 34 | 53 | 61 | 37 | 15 | 2 | 3 | 290 |
| Core* | Large | 15 | 6 | 7 | 19 | 16 | 20 | 20 | 17 | | 1 | 3 | 124 |
| | Small | 1 | 4 | | 2 | 1 | | | | | 1 | | 9 |
| Waste* Flake | Large | 56 | 117 | 56 | 200 | 181 | 229 | 224 | 182 | 68 | 24 | 13 | 1350 |
| | Small | 118 | 79 | 44 | 109 | 129 | 122 | 140 | 136 | 44 | 19 | 12 | 952 |
| Sub-totals | Core & Waste | 190 | 206 | 107 | 330 | 327 | 371 | 384 | 335 | 112 | 45 | 28 | 2435 |
| Totals | Implements & Waste | 216 | 226 | 112 | 364 | 361 | 424 | 445 | 372 | 127 | 47 | 31 | 2725 |

*Cores are graded large or small according to whether their maximum measurement exceeds or falls below 3 cm. Waste flakes are similarly graded as above or below a maximum measurement of 2 cm.

## TABLE 2. SITE BL/1: DISTRIBUTION OF ARTIFACTS BY HORIZONS

| Horizon | Blade, backed | | | | Scraper | | Point, worked | | Flake, Utilized | | Adze Flake | Fabri-cator | Core Util. | Axe Gr. edge | Peb. Util.. | Misc. | Core | | Waste Flake | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Bondi | Elouera | Micro | Other | Side | End | Uni-Face | Other | Blade | Other | | | | | | | Large | Small | Large | Small | |
| 1 | 2 | 1 | 1 | | 6 | 2 | 2 | 4 | | | 3 | 5 | | | | | 15 | 1 | 56 | 118 | 216 |
| 2 | 4 | 3 | | | 7 | | | 2 | | | 2 | 2 | | | | | 6 | 4 | 117 | 79 | 226 |
| 3 | | 1 | | | 1 | | | | | | 1 | 2 | | | | | 7 | | 56 | 44 | 112 |
| 4 | 2 | 3 | 3 | | 9 | | 1 | 3 | | | 4 | 9 | | | | | 19 | 2 | 200 | 109 | 364 |
| 5 | 1 | | 6 | | 3 | 2 | 4 | 5 | | 2 | 3 | 5 | 3 | | | | 16 | 1 | 181 | 129 | 361 |
| 6 | 9 | | 8 | | 5 | | 1 | 15 | | | 5 | 6 | 4 | | | | 20 | | 229 | 122 | 424 |
| 7 | 23 | 1 | 9 | | 5 | 1 | | 14 | | | 7 | | 1 | | | | 20 | | 224 | 140 | 445 |
| 8 | 9 | 1 | 3 | 1 | 7 | | | 10 | | | 2 | 4 | | | | | 17 | | 182 | 136 | 372 |
| 9 | | | 3 | 1 | 3 | | 1 | 3 | | | 4 | | | | | | | | 68 | 44 | 127 |
| 10 | 1 | | | | | | | | | | | | 1 | | | | 1 | 1 | 24 | 19 | 47 |
| 11 | | | | | | | 3 | | | | | | | | | | 3 | | 13 | 12 | 31 |
| Totals | 51 | 10 | 33 | 2 | 46 | 5 | 12 | 56 | — | 2 | 31 | 33 | 9 | — | — | — | 124 | 9 | 1350 | 952 | 2725 |

permission to excavate was obtained from the owners of the property, Messrs Les and Noel Bailey, and a combined Australian Museum and National Parks and Wildlife Service party carried out the excavation during October-November 1970.

Code-named YC/1, this shelter seemed likely to have its maximum depth of deposit in the area of the dripline. A datum was established on a bearing of 242° and a grid laid out on either side of the datum line (see Fig. 2). Square A, just inside the dripline and adjacent to the wombat hole, was commenced. Three-foot squares and three-inch levels were used at this site. In level 2 chert and quartz implements and flakes were found, as well as bone, shell, and charcoal. The deposit was composed of brown to yellow sand, which became progressively yellower in levels 3-4. Broken bone and some small marsupial mandibles continued to appear.

In level 5 the deposit changed immediately to a darker loam. Artifacts increased, but less bone was present. Level 6 was prolific in flakes and blades and in level 7 a huge core of pink quartzite was found at 19 inches. In level 9 the brown humus gave way to yellow sand and artifact yield lessened. In level 11 sloping base rock was reached at 35 inches.

It was decided next to excavate Square DD, just outside the dripline (see Figs. 2 and 11), in the hope that there might be a greater survival of organic material in the damper environment, but in fact the situation closely paralleled that in Square A. When it rained during the course of the excavation, it was found that, due to the conformation of the overhang, there was in fact a subsidiary dripline which passed across the inner edge of Square A. One difference in Square DD was that flaked glass and an old hand-made iron nail were found in level 2 and a further glass flake appeared in level 3. The base rock shelf was reached in level 11 at 38 inches. Although much bone was present in the upper levels, most of it is unidentifiable due to fragmentation. However, the following were identified from mandibular remains: *Macropus gigantea* (Grey Kangaroo) in A/3; *Pseudocheirus peregrinus* (Ringtailed Possum) in A/2; bandicoot spp. in A/4 and A/5; and small reptile spp. in A/4. (Identifications by Mr Basil Marlow, Australian Museum).

The material obtained seemed to provide a sufficient sample of the site. It was subsequently washed and typed and its distribution is shown in Tables 3 and 4. Charcoal from Square A, level 8, was radiocarbon dated to 2350 ± 85 BP (ANU-648), which accords nicely with the dating of the sites in the Hunter Valley itself (SH/1, M/1) and with the amended date for nearby BL/1. Nor was there any feature, in implements or materials, that would immediately distinguish the Wollombi sites from the Hunter Bondaian.

### The Macdonald River Sites

The next area for survey was along the line of the Boree Track, known to have been a traditional Aboriginal route between the Hawkesbury and the Hunter Valleys, as mentioned in the introduction. In fact, local Aborigines are reported to have guided early European settlers into the Wollombi and Howes Valley areas along this route (Sim, 1966) and ruts made by bullock waggons can still be seen on rock sections of the track. The route traversed by the Boree Track is indicated on the map at the beginning of this report. Starting from the south, after a steep initial climb from the valley of Mogo Creek, a tributary of the Macdonald, the track follows high ridges along which there are a series of engravings. About five miles along the track there is a particularly important engraved site, known as Burragurra or the Devil's Rock, and at the northern end is the Finchley's Trig group, previously mentioned. Eventually one branch of the track reaches Mount Yango, which reputedly had a particularly sacred significance for the Aborigines, whence there is an easy route into Howes Valley and on to the Hunter Valley at Milbrodale. Another branch leads into the Wollombi Valley, passing site YC/1 on the way.

It seems likely that the Boree Track was an important ceremonial route, since the

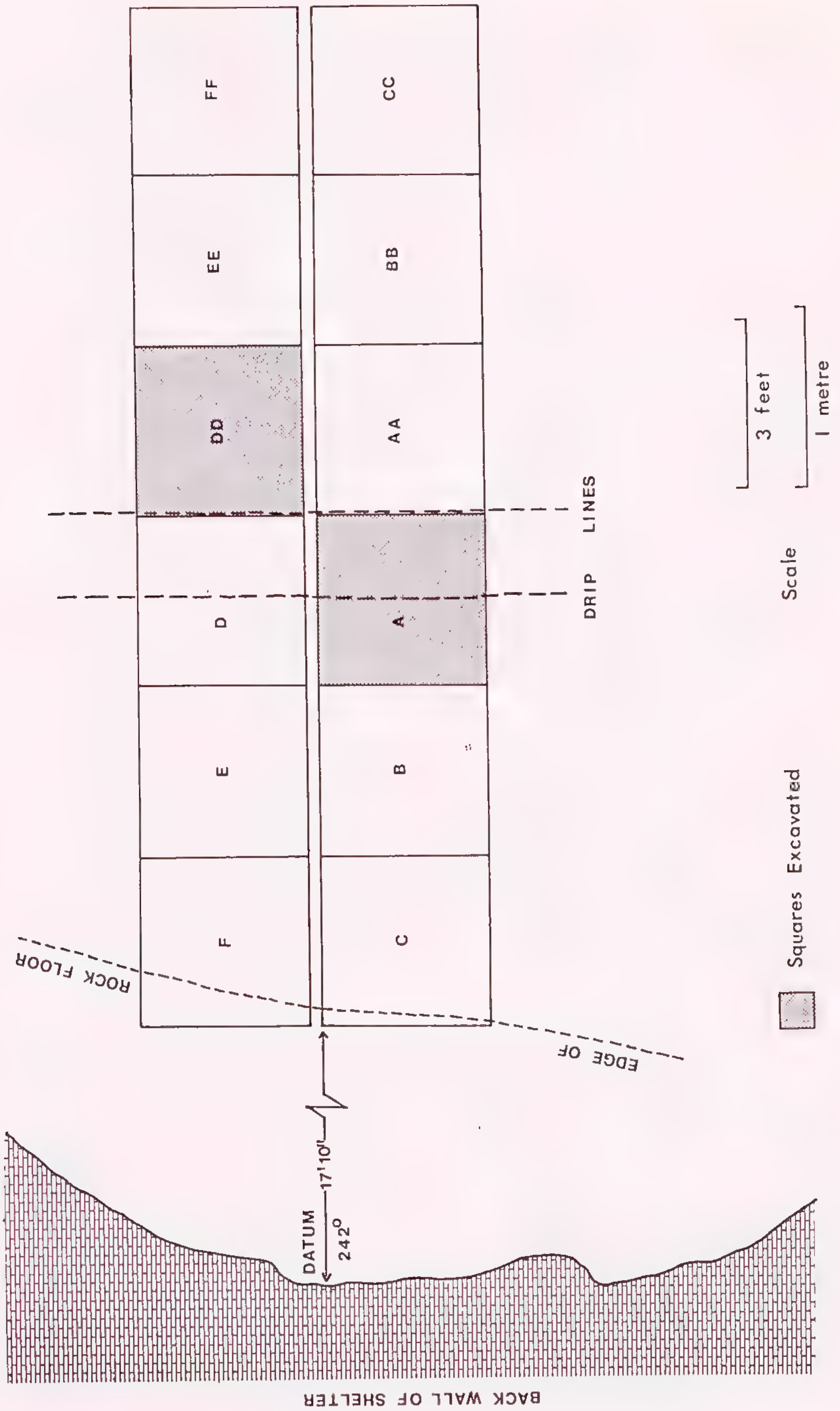

Fig. 2. Site YC/1: grid and excavated area.

engraved sites appear to link up with each other and with Mount Yango (see Sim, 1966). If this is the case, it is extraordinary that Aborigines, even when their culture was disintegrating, should have guided white settlers along it, since legendary paths and initiation grounds were the last things that they would normally reveal to Europeans. From an archaeological point of view the track is not helpful, since there appear to be no occupation sites along it. This is understandable, because of the absence of both water (except for one soak called "Halfway Waterhole") and rock overhangs.

When the Great Northern Road was eventually constructed from Wiseman's Ferry to Wollombi, it avoided the Boree Track, proceeding instead up the Mogo Creek Valley and crossing the watershed near Mount Manning. There are several rock shelters along this route, but most have been interfered with. The painted shelter near Mount Manning excavated by Macintosh (1965) has already been referred to. The deposits were apparently quite shallow with an antiquity of only a few hundred years. The paintings are quite unlike any others in the area. It is possible that the dry and unfruitful country between the Hunter and Hawkesbury Valleys was not penetrated by Aborigines until comparatively recently, whereas occupation of the fertile river valleys took place considerably earlier.

**Site MR/1** (Map: St. Albans, 1-63360). See Fig. 12.

In the absence of any promising sites north of the Macdonald Valley, the survey was extended to the lower reaches of that river, between St. Albans and Wiseman's Ferry. This would most certainly have been Darginung country and it was felt that a stratified site of some antiquity would produce valuable data to compare with that already obtained around Wollombi and in the Hunter Valley itself. It would also be of interest to compare it with the material from site BOB/1, which was just as surely in Gamilaroi territory.

In November 1971 a large shelter, about 200 feet up a steep scarp on the south side of the Macdonald, was found (ref. 969 774). Its roof is about 30 ft. high and the shelter is about 80 ft. long and 20 ft. deep (see Fig. 12). The position of the shelter (code-named MR/1) in relation to the river and scarp is shown schematically in Fig. 3. It contained an extensive occupation deposit which apparently was untouched. Some very faint remains of red ochre paintings only became apparent in the changing light after some time had been spent in sinking a small sondage into the deposits at their western end. This sondage produced a chert flake from about six inches depth and shell and charcoal from about 20 inches.

In March 1972, a datum line having been established on a bearing of 160°, a test square (Square A) was commenced at what appeared to be the deepest part of the deposits, about four feet inside the dripline. Three-foot squares and five-inch levels were used throughout this excavation since no definite stratification appeared. Implement yield in Square A was sparse, but much shell, bone, and charcoal were found down to level 6. A sample of Charcoal from level 5 was submitted to the Sydney University Radiocarbon Laboratory and returned a date of 2370 ± 100 BP (SUA-387).

It was not possible to follow up this promising lead until May 1976, when Square A was completed down to rockfall and coarse sterile sand in level 10 at 50 inches. Charcoal from this level was also processed by the Sydney University Laboratory and dated to 5820 ± 110 BP (SUA-564). This was associated with the earliest artifacts and may be taken to represent approximately the start of occupation of the shelter.

Between August 1976 and January 1977 parties went up to the site by the day to complete a transect of the deposit from back wall out to the external rockfall in front of the shelter. The excavation turned out to be a complicated one, due to the presence of

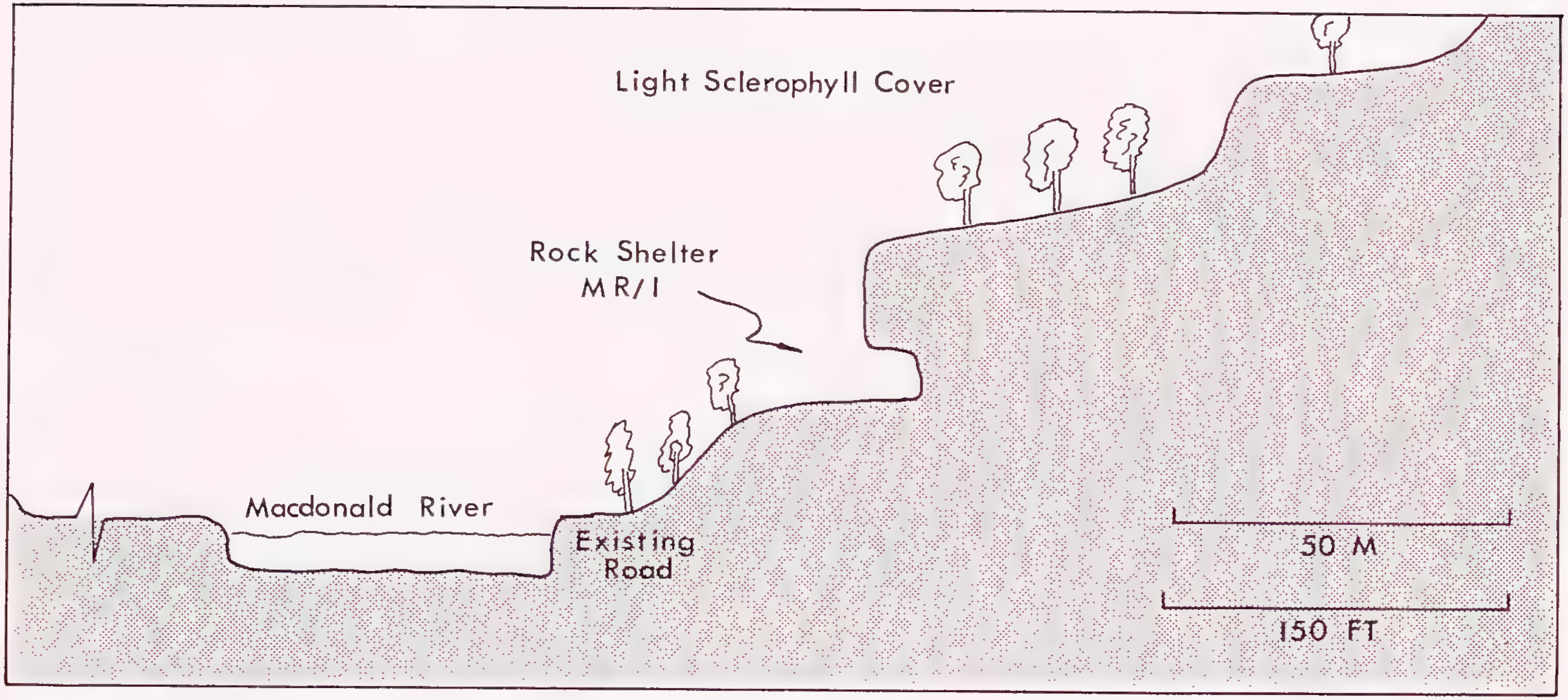

Fig. 3. Site MR/1: profile of shelter and valley.

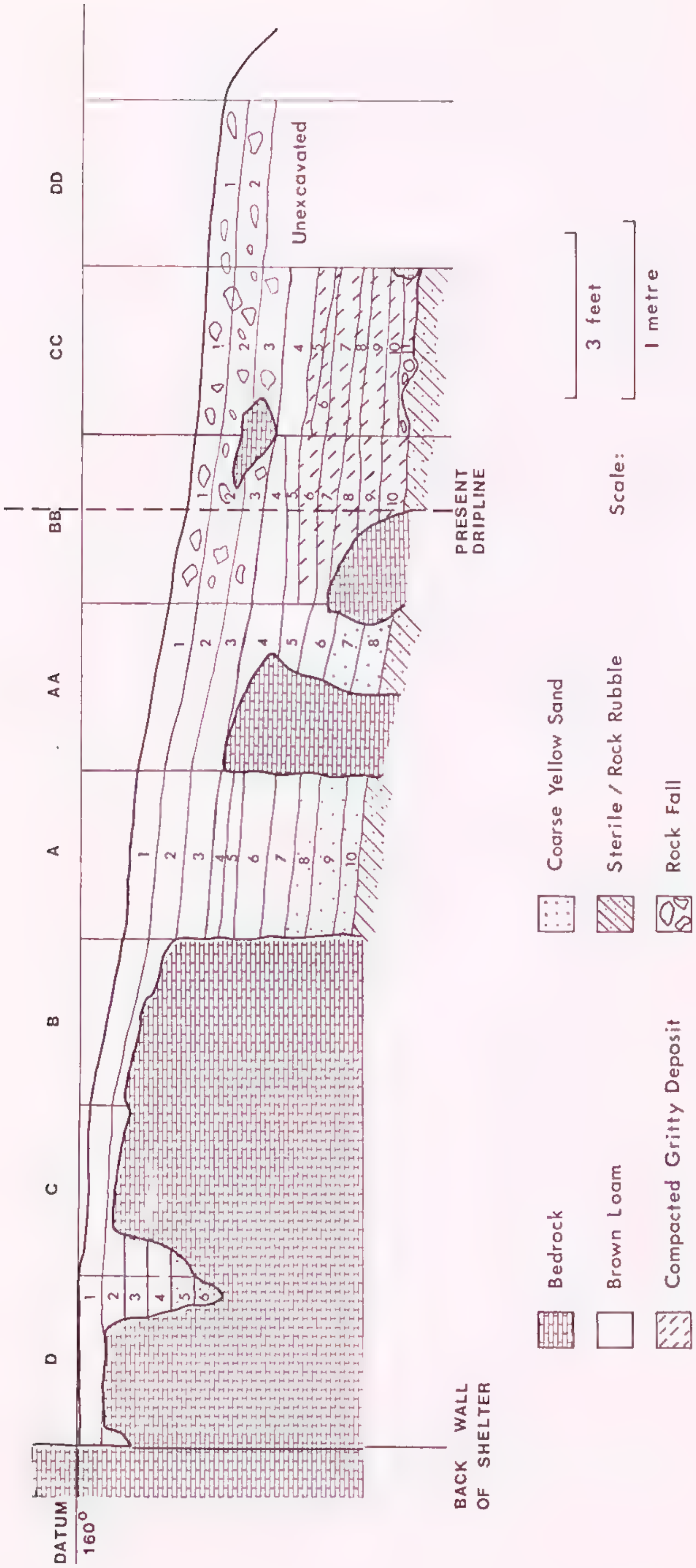

Fig. 4. Site MR/1: section of deposits.

irregular masses of base rock and rockfall, as may be seen in the section illustrated in Fig. 4. Square A had gone precisely into a deep cavity in the rock floor, but the inner squares, B, C, and D, were only a few inches deep, apart from some clefts in the base rock. Nevertheless, they contained significant quantities of artifacts, including backed blades. (See Fig. 13.)

When Square AA was commenced it produced plenty of flakes and shell but a very sparse yield of implements. In level 4 a rock ledge was encountered in the southern half of the square, but the deposit continued in the remainder. At the end of level 5 it was too constricted to continue until Square BB had been partially excavated. Meanwhile Square DD, outside the dripline, was commenced, but after two levels had been dug and nothing found but rockfall, it was abandoned and Square BB was excavated across the dripline. Much rockfall was met within the northern half, but the deposit continued with a sparse yield of flakes and implements. At 15-18 inches several flaked pieces of a diorite edge-ground axehead were found and subsequently other fragments were found at similar depths in other squares. Some small "unipoints" of bone and a very large worked bone point were found at 21 inches. In level 5 Square BB went into soft loam with some compacted areas and at the end of level 6 became more compacted and gritty with many chunks of decomposing sandstone.

At this point Square AA was continued beside and under the rock in the southern half. Artifacts continued into coarse yellow sand, which then became sterile. Square BB was continued into rockfall in level 10, artifacts, including Bondi points, appearing throughout.

It was then obvious that Square CC must be dug to complete the transect, and subsequently many artifacts were found, mixed with tumbled rock. Level 4 was particularly prolific, six Bondis being found within a small area in the south-west quadrant. Rockfall lessened in the lower levels, but bone and shell no longer appeared. Square CC went into rubble in level 10 and met bedrock in level 11, but produced backed blades to the end (see Fig. 13).

The extensive rockfall in the upper levels of Squares CC and DD was assumed to represent the disintegration of an earlier extension of the overhang and it was thought this might indicate that the occupation of this zone was earlier than that inside the present overhang, so charcoal from BB/10 and CC/8-9-10 was submitted to the Sydney University laboratory. The scarcity of charcoal in this zone necessitated this grouping of levels. The combined samples returned a date of 3650+ 130 BP (SUA-676) which indicates that occupation of all zones, both inside and outside the present overhang, was contemporaneous.

The distribution of implements and waste is shown by squares and levels in Table 5 and by horizons in Table 6. However, it should be realised that correlation of levels was extremely difficult in this excavation, due to the complicated series of rock slabs, so that the attribution of both levels and horizons can only be approximate.

Both shell and bone were present in varying quantities in the first seven levels of Squares A, AA, BB, and CC. The shell was almost entirely estuarine mussel *(Trichomya hirsuta)*, but an occasional rock oyster *(Soccostrea commercialis)* appeared. The absence of shell from the earlier levels may be due to decomposition over a greater time-span or may mean that mussel was not being collected. Nowadays the Macdonald is affected up as far as MR/1 by high tides and is usually somewhat brackish at that point, but it has greatly silted up since settlement, due to progressive clearing of cover and the resulting increase in soil erosion. Probably in Aboriginal times it was salt up to about the present

## TABLE 3. SITE YC/1: DISTRIBUTION OF STONE IMPLEMENTS AND WASTE

| Square | | A | | | | | | | | | | | | | DD | | | | | | | | | | | | Grand Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Level | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | Total | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | Total | |
| Blade, backed | Bondi | | | | | 3 | 5 | 10 | 2 | 3 | 4 | | | 27 | | 2 | 2 | 10 | 9 | 3 | 2 | 2 | | | | 30 | 57 |
| | Elouera | | | | | | | | 1 | | | | | 1 | | | | 2 | | 3 | | | | | | 5 | 6 |
| | Microlith | | | | | 3 | 4 | 6 | 6 | 4 | | | | 23 | | | | 6 | 2 | 9 | 4 | 5 | 2 | 2 | 1 | 31 | 54 |
| | Other | | | | | | 2 | | 2 | | | | | 4 | | | | | | | | | | | | | 4 |
| Scraper | Side | | | | | | 4 | 5 | 3 | | | | | 12 | | | 4 | 13 | 7 | 6 | 2 | | | | | 32 | 44 |
| | End | | | | 1 | | | | | 2 | 1 | | | 4 | | | 1 | | 7 | 2 | 1 | | | | | 11 | 15 |
| Point, worked | Uniface | | | | | | | 3 | | | | | | 3 | | | | 7 | | 1 | | | | | | 8 | 11 |
| | Other | | | | | 3 | 7 | 3 | 7 | 1 | 1 | | | 22 | | 1 | 5 | 8 | 5 | 2 | 2 | 2 | 1 | | | 26 | 48 |
| Flake, utilized | Blade | | | | | | 2 | | 1 | | | | | 3 | | | | | 3 | 1 | | | | | | 4 | 7 |
| | Other | | | | | | | | 1 | | | | | 1 | | | | | | | | | | | | | 1 |
| | Adze flake | | | | | 2 | 3 | 4 | 5 | 1 | | | | 15 | | | 2 | 6 | 1 | | 2 | | | | | 11 | 26 |
| | Fabricator | | | | 1 | | | | | | | | | 1 | | | | 4 | 1 | 1 | 1 | | | | | 7 | 8 |
| | Core, utilized | | | | | | | | | | | | | | | | | 1 | | | | | | | | 1 | 1 |
| | Axe, gr. edge | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Pebble, utilized | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Miscellaneous | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Sub-totals | Implements | | | | 2 | 11 | 27 | 31 | 28 | 11 | 6 | | | 116 | | 3 | 14 | 57 | 35 | 28 | 14 | 9 | 3 | 2 | 1 | 166 | 282 |
| Core | Large | | 2 | 6 | 1 | 16 | 15 | 21 | 18 | 4 | 3 | 1 | | 87 | 1 | 2 | 14 | 28 | 26 | 24 | 7 | 7 | 1 | 3 | 3 | 116 | 203 |
| | Small | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 | 1 |
| Waste flake | Large | 2 | 10 | 10 | 3 | 160 | 192 | 244 | 188 | 75 | 27 | 4 | 1 | 916 | 4 | 8 | 86 | 518 | 238 | 227 | 89 | 44 | 11 | 11 | 5 | 1241 | 2157 |
| | Small | 7 | 21 | 12 | 4 | 64 | 85 | 94 | 152 | 78 | 23 | 19 | 4 | 563 | 18 | 13 | 41 | 103 | 178 | 136 | 75 | 14 | 7 | 5 | 5 | 595 | 1158 |
| Sub-totals | Core & Waste | 9 | 33 | 28 | 8 | 240 | 292 | 359 | 358 | 157 | 53 | 24 | 5 | 1566 | 23 | 23 | 141 | 649 | 442 | 388 | 171 | 65 | 19 | 19 | 13 | 1953 | 3519 |
| Totals | Implements & Waste | 9 | 33 | 28 | 10 | 251 | 319 | 390 | 386 | 168 | 59 | 24 | 5 | 1682 | 23 | 26 | 155 | 706 | 477 | 416 | 185 | 74 | 22 | 21 | 14 | 2119 | 3801 |

## TABLE 4. SITE YC/1: DISTRIBUTION OF ARTIFACTS BY HORIZONS

| Horizon | Blade, backed | | | | Scraper | | Point, worked | | Flake, Utilized | | Adze Flake | Fabri-cator | Core Util. | Axe Gr. edge | Peb Util. | Misc. | Core | | Waste Flake | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Bondi | Elouera | Micro | Other | Side | End | Uni. Face | Other | Blade | Other | | | | | | | Large | Small | Large | Small | |
| 1 | | | | | | | | | | | | | | | | | 1 | | 6 | 25 | 32 |
| 2 | 2 | | | | | | | 1 | | | | | | | | | 4 | | 18 | 34 | 59 |
| 3 | 2 | | | | 4 | 1 | | 5 | | | 2 | | | | | | 20 | | 96 | 53 | 183 |
| 4 | 10 | 2 | 6 | | 13 | 1 | 7 | 8 | | | 6 | 5 | 1 | | | | 29 | | 521 | 107 | 716 |
| 5 | 12 | | 5 | | 7 | 7 | | 8 | 3 | | 3 | 1 | | | | | 42 | | 398 | 242 | 728 |
| 6 | 8 | 3 | 13 | 2 | 10 | 2 | 1 | 9 | 3 | | 3 | 1 | | | | | 39 | 1 | 419 | 221 | 735 |
| 7 | 12 | 1 | 10 | | 7 | 1 | 3 | 5 | | | 6 | 1 | | | | | 28 | | 333 | 169 | 576 |
| 8 | 4 | | 11 | 2 | 3 | | | 9 | 1 | | 5 | | | | | | 25 | | 232 | 166 | 458 |
| 9 | 3 | | 6 | | | 2 | | 2 | | 1 | 1 | | | | | | 5 | | 86 | 85 | 191 |
| 10 | 4 | | 2 | | | 1 | | 1 | | | | | | | | | 6 | | 38 | 28 | 80 |
| 11 | | | 1 | | | | | | | | | | | | | | 4 | | 9 | 24 | 38 |
| 12 | | | | | | | | | | | | | | | | | | | 1 | 4 | 5 |
| Totals | 57 | 6 | 54 | 4 | 44 | 15 | 11 | 48 | 7 | 1 | 26 | 8 | 1 | — | — | — | 203 | 1 | 2157 | 1158 | 3801 |

## TABLE 5. SITE MR/1: DISTRIBUTION OF STONE IMPLEMENTS AND WASTE

| | Square | A | | | | | | | | | | | B | | | C | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Level | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Total | 1 | 2 | Total | 1 | 2 | 3 | 4 | 5 | Total |
| Blade, backed | Bondi | 1 | 1 | | | | 1 | 1 | | 2 | | 6 | | | | | | 2 | 2 | | 4 |
| | Elouera | | | | | | | | | | | | | | | | | | | | |
| | Microlith | | | | | | 1 | | | | | 1 | | | | | | | | | |
| | Other | | | | | | | | | | | | | | | | | | | | |
| Scraper | Side | 1 | 1 | | | | 4 | 2 | 1 | 3 | | 12 | | | | | | | | 1 | 1 |
| | End | | | | | | | | | | | | | | | | 1 | | | | 1 |
| Point, worked | Uni-face | | | | | | | | | | | | | | | | | | | 1 | 1 |
| | Other | | | | | | | | | | | | | | | | | | | | |
| Flake, utilized | Blade | | | | | | | | | | | | | | | | | | | | |
| | Other | | | | | | | | | | | | | | | | | | | | |
| | Adze flake | | | | | | | | | 1 | | 1 | | | | | | | | | |
| | Fabricator | | 2 | | | 3 | 1 | | 2 | 1 | | 9 | 1 | | 1 | 1 | | 1 | 1 | | 3 |
| | Core, utilized | | | | | | | | | 1 | | 1 | | | | | | | | | |
| | Axe, gr. edge | | | | | | | | | | | | | | | | | | | | |
| | Pebble, utilized | | | | | | | | | | | | | | | | | | | | |
| | Miscellaneous | | | | | | | | | | | | 2 | | 2 | | 1 | | | | 1 |
| Sub-Totals | Implements | 2 | 4 | | | 3 | 7 | 3 | 3 | 8 | | 30 | 3 | | 3 | 1 | 2 | 3 | 3 | 2 | 11 |
| Core | Large | 2 | 8 | | 1 | 4 | 4 | 7 | 7 | 6 | 8 | 47 | 2 | 3 | 5 | 2 | 4 | 3 | 5 | 1 | 15 |
| | Small | | 1 | | 1 | 3 | 2 | 1 | | 1 | | 9 | 1 | 2 | 3 | 4 | | 1 | | | 5 |
| Waste Flake | Large | 16 | 22 | 1 | 3 | 22 | 40 | 1 | 57 | 48 | 23 | 233 | 16 | 30 | 46 | 53 | 11 | 39 | 42 | 23 | 168 |
| | Small | 10 | 10 | | | 7 | 15 | 7 | 20 | 15 | 7 | 91 | 10 | 17 | 27 | 21 | 1 | 6 | 13 | 3 | 44 |
| Sub-Totals | Core & Waste | 28 | 41 | 1 | 5 | 36 | 61 | 16 | 84 | 70 | 38 | 380 | 29 | 52 | 81 | 80 | 16 | 49 | 60 | 27 | 232 |
| Totals | Implements & Waste | 30 | 45 | 1 | 5 | 39 | 68 | 19 | 87 | 78 | 38 | 410 | 32 | 52 | 84 | 81 | 18 | 52 | 63 | 29 | 243 |

*TABLE 5 Cont.*

| Square | | D | | | | | | | AA | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Level | 1 | 2 | 3 | 4 | 5 | 6 | Total | 1 | 2 | 3 | 4 | 5 | 6 | 7/8 | Total |
| Blade, backed | Bondi | | 1 | | 2 | 3 | 1 | 7 | 1 | 1 | 1 | 1 | | | 2 | 6 |
| | Elouera | | | | | | | | | | | | | | | |
| | Microlith | | 1 | | | 3 | | 4 | | | | | | 1 | 1 | 2 |
| | Other | | | | | | | | | | | | | | | |
| Scraper | Side | 2 | 1 | | 1 | 1 | | 5 | | | | | 1 | | 2 | 3 |
| | End | | | | | | | | | | | | | | | |
| Point, worked | Uni-face | | | | | | | | | | 1 | | | | 1 | 2 |
| | Other | | | | | | | | | | | | | | | |
| Flake, utilized | Blade | | | | | | | | | | | | | | | |
| | Other | | | | | | | | | | | | | | | |
| | Adze flake | | | | | | | | | | | | | | | |
| | Fabricator | | | 1 | | 1 | | 2 | 1 | | 3 | | 1 | | | 5 |
| | Core, utilized | | | | | | | | | | | | | | 1 | 1 |
| | Axe, gr. edge | | | | | | | | | | | | | | | |
| | Pebble, utilized | | | | | | | | | | | | | | | |
| | Miscellaneous | 3 | | | | | | 3 | | 3 | | | | | 1 | 4 |
| Sub-Totals | Implements | 5 | 3 | 1 | 3 | 8 | 1 | 21 | 2 | 4 | 5 | 1 | 2 | 1 | 8 | 23 |
| Core | Large | 6 | 3 | 3 | 5 | 10 | 2 | 29 | 1 | | 3 | 5 | 5 | 4 | 2 | 20 |
| | Small | | 1 | 2 | 1 | 1 | | 5 | | 1 | | | | | | 1 |
| Waste Flake | Large | 32 | 19 | 16 | 62 | 41 | 5 | 175 | 37 | 26 | 46 | 33 | 13 | 33 | 65 | 253 |
| | Small | 12 | 3 | 5 | 21 | 22 | 2 | 65 | 11 | 6 | 12 | 5 | 4 | 7 | 16 | 61 |
| Sub-Totals | Core & Waste | 50 | 26 | 26 | 89 | 74 | 9 | 274 | 49 | 33 | 61 | 43 | 22 | 44 | 83 | 335 |
| Totals | Implements & Waste | 55 | 29 | 27 | 92 | 82 | 10 | 295 | 51 | 37 | 66 | 44 | 24 | 45 | 91 | 358 |

**TABLE 5 Cont.**

| Square | | BB | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Level | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Total |
| Blade, backed | Bondi | | | | 3 | 1 | 1 | | 2 | 1 | 6 | 14 |
| | Elouera | | | | | | | | | | 2 | 2 |
| | Microlith | | | | | | 1 | | | 1 | | 2 |
| | Other | | | | | | | | | | | |
| Scraper | Side | | | | | | | | | | | |
| | End | | | | | | | | | | | |
| Point, worked | Uni-face | | | | | | | | | | | |
| | Other | | | | | | | | | | | |
| Flake, utilized | Blade | | | | | | | | | | | |
| | Other | | | | | | | | | | 1 | 1 |
| | Adze flake | | | | | | | | | | | |
| | Fabricator | | 3 | 1 | 2 | 3 | 2 | 2 | 2 | 1 | | 16 |
| | Core, utilized | | | | 1 | | | | | | | 1 |
| | Axe, gr. edge | | | | | | | | | | | |
| | Pebble, utilized | | | | | | | | | | | |
| | Miscellaneous | | 6 | 6 | 2 | 4 | | | 3 | | | 21 |
| Sub-Totals | Implements | | 9 | 7 | 8 | 8 | 4 | 2 | 7 | 3 | 9 | 57 |
| Core | Large | 3 | 4 | 4 | 10 | 4 | 6 | 4 | 8 | 4 | 1 | 48 |
| | Small | | | | | | 1 | | | | | 1 |
| Waste Flake | Large | 4 | 28 | 29 | 59 | 53 | 104 | 62 | 109 | 50 | 30 | 528 |
| | Small | 2 | 7 | 8 | 6 | 5 | 17 | 17 | 23 | 17 | 4 | 106 |
| Sub-Totals | Core & Waste | 9 | 39 | 41 | 75 | 62 | 128 | 83 | 140 | 71 | 35 | 683 |
| Totals | Implements & Waste | 9 | 48 | 48 | 83 | 70 | 132 | 85 | 147 | 74 | 44 | 740 |

TABLE 5 Cont.

| Square | | CC | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Level | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | Total | Grand Total |
| Blade, backed | Bondi | | 1 | 2 | 7 | | | 5 | 1 | 2 | 2 | | 20 | 57 |
| | Elouera | | | | 1 | | | 1 | | | | | 2 | 4 |
| | Microlith | | | | | 1 | | 2 | | | | | 3 | 12 |
| | Other | | | 1 | 1 | 1 | | | | | | | 3 | 3 |
| Scraper | Side | | 1 | 1 | 2 | 1 | | 1 | | 1 | 1 | | 8 | 29 |
| | End | | | | 1 | | | | | | | | 1 | 2 |
| Point, worked | Uni-face | | | | | | | | | | | | | 3 |
| | Other | | | | | | | | | | | | | |
| Flake, utilized | Blade | | | | | | | | | | | | | |
| | Other | | | | 1 | | | | | | | | 1 | 2 |
| | Adze flake | | | | | | | | 1 | | | | 1 | 2 |
| | Fabricator | | 1 | 3 | 8 | 1 | 2 | 3 | 5 | 1 | | | 24 | 60 |
| | Core, utilized | | | | | 1 | | | | 1 | 1 | 1 | 4 | 7 |
| | Axe, gr. edge | | | | | | | | | | | | | |
| | Pebble, utilized | | | | | | | | | | | | | |
| | Miscellaneous | | | 8 | 4 | | | | | | | | 12 | 43 |
| Sub-Totals | Implements | | 3 | 15 | 25 | 5 | 2 | 12 | 7 | 5 | 4 | 1 | 79 | 224 |
| Core | Large | 1 | 2 | 14 | 50 | 14 | 11 | 5 | 3 | 8 | 4 | 4 | 115 | 280 |
| | Small | | 2 | 3 | 8 | 1 | 1 | 3 | 2 | | 3 | | 23 | 47 |
| Waste Flake | Large | 14 | 48 | 271 | 1003 | 320 | 194 | 117 | 116 | 78 | 11 | 26 | 2198 | 3601 |
| | Small | 1 | 13 | 49 | 202 | 39 | 20 | 23 | 21 | 13 | 14 | 4 | 399 | 793 |
| Sub-Totals | Core & Waste | 16 | 65 | 337 | 1263 | 374 | 226 | 148 | 142 | 99 | 32 | 34 | 2736 | 4721 |
| Totals | Implements & Waste | 16 | 68 | 352 | 1288 | 379 | 228 | 160 | 149 | 104 | 36 | 35 | 2815 | 4945 |

## TABLE 6. SITE MR/1: DISTRIBUTION OF ARTIFACTS BY HORIZONS

| Horizon | Blade, backed | | | | Scraper | | Point, worked | | Flake Utilized | | Adze Flake | Fabri-cator | Core Utilized | Axe Gr. Ed. | Pebble Utilized | Misc. | Core | | Waste Flake | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Bondi | Elouera | Micro | Other | Side | End | Uni-Face | Other | Blade | Other | | | | | | | Large | Small | Large | Small | |
| 1 | 2 | | | | 3 | | | | | | | 3 | | | | 5 | 17 | 5 | 172 | 67 | 274 |
| 2 | 4 | | 1 | | 3 | 1 | | | | | | 6 | | | | 10 | 24 | 7 | 184 | 57 | 297 |
| 3 | 5 | | | 1 | 1 | | 1 | | | | | 9 | | | | 14 | 27 | 6 | 402 | 80 | 546 |
| 4 | 15 | 1 | | 1 | 3 | 1 | | | | 1 | | 11 | 1 | | | 6 | 76 | 10 | 1202 | 247 | 1575 |
| 5 | 4 | | 4 | 1 | 4 | | 1 | | | | | 9 | 1 | | | 4 | 38 | 5 | 472 | 80 | 623 |
| 6 | 3 | | 3 | | 4 | | | | | | | 5 | | | | | 27 | 4 | 376 | 61 | 483 |
| 7 | 8 | 1 | 3 | | 5 | | 1 | | | | | 5 | 1 | | | 1 | 18 | 4 | 245 | 63 | 355 |
| 8 | 3 | | | | 1 | | | | | | 1 | 9 | | | | 3 | 18 | 2 | 282 | 64 | 383 |
| 9 | 5 | | 1 | | 4 | | | | | | 1 | 3 | 2 | | | | 18 | 1 | 176 | 45 | 256 |
| 10 | 8 | 2 | | | 1 | | | | | 1 | | | 1 | | | | 13 | 3 | 64 | 25 | 118 |
| 11 | | | | | | | | | | | | | 1 | | | | 4 | | 26 | 4 | 35 |
| Totals | 57 | 4 | 12 | 3 | 29 | 2 | 3 | — | — | 2 | 2 | 60 | 7 | — | — | 43 | 280 | 47 | 3601 | 793 | 4945 |

Note: Artifacts listed under AA7/8 in Table 5 have been included in Horizon 7 in this table.

site of St Albans, so the mussel represented in the MR/1 deposits may well have been collected in the vicinity of the shelter.

Most of the shell found was very fragmented, so it is not possible to estimate the number of shells present. For this reason comparative occurrence has been measured by weight and by horizon, as is shown in Table 7.

**TABLE 7. SITE MR/1. COMPARATIVE OCCURRENCE OF SHELL (BY HORIZONS)**

| Horizon | Weight (gm) |
|---|---|
| 1 | 2 |
| 2 | 2.5 |
| 3 | 7 |
| 4 | 4.5 |
| 5 | 4 |
| 6 | 1.5 |
| 7 | 2 |
| 8-11 | nil |

Other fauna were represented in Squares AA and BB, levels 3-6, but are not identifiable even to generic level, due to extreme fragmentation of the bone. However, the following were certainly present: wallaby; large bird; large fish.

It is clear that the subsistence strategy of the people using this site was a wide-ranging one, exploiting river, valley, and scarp resources simultaneously. Due to lack of time and facilities, it was not possible to check the deposits for possible pollen survival, so that no estimate of the plant component of the diet can be made, but it may be assumed to have been considerable, in the context of the fertile river valley systems of the Macdonald and Hawkesbury. Not more than one-tenth of the total occupation deposit in MR/1 was excavated during this survey, so it can be further investigated in the future.

During the period of excavation of MR/1 a number of reconnaissances were made in the locality and some well preserved cave paintings were discovered about five miles upstream. They are in a huge hollow boulder (MR/2) lying about 500 feet up a moderately sloping hillside on the east side of the Macdonald (ref. 984844). They include what appears to be a turtle, outlined in white and infilled with a grid pattern in white, several lines of small dancing men, together with some individual human figures in white ochre and charcoal, and, interestingly, a radiate design and "tally marks" in white, similar to those around Wollombi (see Fig. 14). A sondage into the deposit in this shelter showed it to be completely sterile.

During a reconnaissance along the top of the scarp above MR/1 a stone arrangement was found which encloses two small natural rock basins, one permanently filled with water from a spring and the other dry (ref. 962773). The arrangement is composed of natural stones piled up into a low wall enclosing an oval area 90 feet long and 20 feet wide. It seems unlikely to have been made by European settlers, since it would be no barrier to cattle or sheep, and may possibly be the remains of a bora or initiation ground. No implements of any sort were found during these investigations of the top of the scarp, but quartz nodules, similar to material used for flaking at Site MR/1, were found to occur frequently in the sandstone conglomerate.

Before proceeding to a consideration of the comparative analysis of artifacts from these excavations, attention should be drawn to the tables showing the distribution of artifacts for sites BL/1, YC/1, and MR/1. It will be noticed that at site BL/1 the maximum occurrence was in horizon 7, at YC/1 in horizon 6, and at MR/1 in horizon 4. If we extrapolate from the levels carbon-dated, as was done in Part I of this survey, we find that horizon 7 at BL/1 dates to about 1800-2300 BP, horizon 6 at YC/1 to about 1700-2000 BP and horizon 4 at MR/1 to around 1800-2300 BP. (It should be noted that BL/1 and YC/1 were excavated in 3-inch levels, whereas 5-inch levels were used at MR/1, so the difference in rate of deposition is not as marked as might be supposed.) It seems, then, that around 1800-2000 BP was a period of maximum activity at sites at both ends of the Boree Track.

The implications of this apparent pattern will be considered further when the results of materials and computer analysis have been described.

## MATERIALS AND COMPUTER ANALYSIS

The range of lithic materials used for flaking at the MR/1 site was much wider than at any of the other sites excavated during the survey. Since the only material suitable for flaking found in the locality was the very variable quartz present in nodular form in the sandstone conglomerate of the scarps, this seemed to imply an extensive trade in raw material for tool-making. Analysis of the stone types present in the implements and waste excavated at MR/1 was therefore undertaken and an estimate of possible sources made, with the assistance of Professor D. Branagan, Department of Economic Geology, University of Sydney. The materials present (excluding quartz, which is almost impossible to provenance) appear to group at an elementary level as follows:

| *Material* | *Description* | *Possible Source* |
|---|---|---|
| Chert/Jaspar | Yellow/Red | Hunter/Goulburn |
| Chert | Lt Grey/White | Merewether, Newcastle |
| Chert | Dark Grey/Black | Wagonga, S. Coast |
| Quartzite* | Grey/Yellow | Doubtful |
| Quartzite* | Pink/Red | Hunter |
| Igneous | Diorite | New England |

*These two categories could possibly be identified as silcretes, but the term quartzite is usually applied to them in Australia.

The following chart (Table 8) shows the distribution of material at MR/1 by horizons. Only implements are included in this analysis and identifications are tentative only. Nevertheless some apparent patterns do appear.

**TABLE 8 . SITE MR/1: DIFFERENTIATION OF MATERIAL BY HORIZONS (IMPLEMENTS ONLY. N = 155)**

| HORIZON | Chert Yellow/ Red | Chert Lt Grey/ White | Chert Dk Grey/ Black | Quartzite Grey/ Yellow | Quartzite Pink/ Red | Igneous Diorite (Grd flakes) |
|---|---|---|---|---|---|---|
| 1 | ** |  | * | ** | * | **** |
| 2 | ** | *** |  |  | *** | *****<br>***** |
| 3 | * | * | *** | * | **** | *****<br>* |
| 4 | ** | *****<br>** | **** | *****<br>**** | ***** | * |
| 5 | ***** | ***** | ** | *** | *** | *** |
| 6 | * | ** | *** | **** | * |  |
| 7 | *** | **** | *** | ***** | *****<br>* |  |
| 8 |  |  |  | *** | ** |  |
| 9 | *****<br>** |  |  | *** | ** |  |
| 10 | * | ** |  | *****<br>*** | * |  |
| 11 |  | * |  |  |  |  |

Note: Quartz implements not included, since it is impossible to localise sources.

It will be noticed that the putative Hunter Valley cherts (col. 1), Merewether chert (col. 2), and Hunter quartzites (col. 5) appear throughout the time span of occupation, whereas the possible Wagonga black cherts come in only in horizon 7 (i.e. at about 3000 BP). Similarly the diorite flakes (all of which had ground facets) come in at horizon 5 (i.e. at about 2400 BP). This would seem to imply that at the time of first occupation (about 6000 BP) contacts were purely local, but that a widespread trading network developed between 3000 and 2000 BP. The grey/yellow quartzites, which have not been localised, appear most strongly in horizons 4-10, but are present throughout the deposits; it is possible that they are derived from a source in the vicinity of the Macdonald Valley which has not yet been discovered.

It should be added that single specimens of black chert appeared in the waste from levels 9 and 10 in Square CC only. In view of the dating for this zone (SUA-676) this does not necessarily invalidate the suggestions made above. No diorites appear in the waste earlier than horizon 5, though dolerites are present in the lower levels. These are possibly from the northern fringes of the Hunter Valley, but not from as far afield as New England.

At the conclusion of the excavations early in 1977, it was decided to attempt to extract additional facets of information from the extensive sample of Bondi points obtained from the totality of the excavated sites. The help of the C.S.I.R.O. Computing Research Centre in the University of Sydney was enlisted and David Hain, a programmer who was also studying anthropology and archaeology, agreed to undertake the project. The summaries of computer printouts listed below have all been supplied by him, but the comments and interpretations are the result of discussions between David Hain, Ian Johnson, and the author.

The basic descriptive categories employed in the computer project were identical with those used in the statistical analyses in Part I of this report, i.e. maximum length, maximum breadth, thickness at mid point, weight, and cutting angle at mid point of the chord.

In order to include a coastal sample in the programme, backed blades were included from two surface sites extensively collected by L. K. Dyall — Williamtown Road (Map: Newcastle, 1-63360, ref. 886442) and Swansea Heads (Map: Lake Macquarie, 1-63360, ref. 664084). These sites have already been referred to in the section on the Hunter estuary. All undamaged Bondi points from these two sites were extracted and measured by the same methods used on the excavated collections. These two Dyall sites were code-named WR/1 (Williamtown Road) and LM/1 (Lake Macquarie).

The dichotomy between quartz implements and those made of cherts or quartzites soon became apparent in the computer programmes, as it did in the statistical comparisons in the first part of this report. However, the division was not made completely until late in the computer project, when it became clear that the marked differences in the quartz samples were tending to obscure the key issues.

Originally it was hoped to analyse any areal variations present in the implements, both synchronically and diachronically. Initially the total samples from all sites were included and the complexities and problems encountered in the earlier stages of the project made it premature to attempt any cross-site analyses by horizons or by dated levels.

The programmes employed initially were all taxonomic and had proved successful in applications for analyses of natural history collections. However, the size of the sample, the number of attributes included, and the very variable occurrence of quartz made interpretation of the printouts virtually impossible. There appeared to be no consistency in the attributes contributing to the various groupings, nor was there any indication of grouping by sites. At this point in the project it appeared that the distribution was almost entirely a random one. One indication did, however, stand out — the Bondi points from Dyall's two coastal sites were markedly larger (and correspondingly heavier) than those from the middle Hunter and other inland sites.

At this point advice was sought from Ian Johnson, who had had wide experience of computer applications to archaeological data in Europe and was, in fact, incorporating the Hunter statistics into his own Ph.D. research programme, on the interface between the Capertian and Bondaian phases in eastern New South Wales. He recommended switching to discriminant analysis and it was decided to try an alternative approach. The new programmes used were those described in SPSS (*Statistical Package for the Social Sciences*, by Nie, Hull, *et al*, 2nd edition, 1975). The selection method used was RAO's V — a generalised distance measure (as described on page 448 of SPSS). This was the point at which it was decided again to separate quartz and non-quartz, in order to give the new approach every chance of success.

The results of the various runs are summarised in the following paragraphs. The original printouts are included in the survey material deposited in the Anthropology Department of the Australian Museum and may be studied there.

(i) *All tools, both quartz and non-quartz; all sites*
Variables: length, breadth, thickness, weight, cutting angle.
Result: 32 per cent of tools correctly classified as to provenance.
Main discriminators: length, weight, cutting angle.

(ii) *All non-quartz tools; all sites*
Variables: length, breadth, thickness, weight, cutting angle.
Result: 34 per cent correctly classified as to provenance.
Main discriminators: length, weight, cutting angle.

(iii) *All non-quartz tools; all sites, but WR/1 and LM/1 grouped*
Variables: length, breadth, thickness, weight, cutting angle.
Result: 37 per cent correctly classified as to provenance.
Main discriminators: length, weight, cutting angle.

(iv) *All non-quartz tools; sites SH/1, MR/1, M/1, YC/1, BL/1*
Variables: all attributes used.
Result: 46 per cent correctly classified as to provenance.
Main discriminators: cutting angle, thickness, weight.
(Note: SH/1 was 60 per cent correctly classified and MR/1 was 55 per cent correctly classified.)

(v) *All non-quartz tools; sites SH/1, MR/1, M/1, YC/1, BL/1, (WR/1, LM/1 grouped)*
Variables: all attributes used.
Result: 51 per cent correctly classified as to provenance.
Main discriminators: Weight, length, cutting angle.

(vi) *All non-quartz tools; sites as in (v)*
Variables: length, weight, cutting angle.
Result: 49 per cent correctly classified as to provenance.
(Note: the slight difference in this result, as compared with (v) — 49 per cent as against 51 per cent — indicates that width and thickness play little part in selection by discriminant analysis.)

(vii) *All non-quartz tools; sites as in (v)*
Variables: length, weight.
Result: 38 per cent correctly classified as to provenance.
(Note: this result, when compared with (v) and (vi) — 51 per cent and 49 per cent — indicates that cutting angle is the third most important discriminator.)

(viii) *All non-quartz tools; all sites except coastal (WR/1, LM/1)*
Variables: all attributes used.
Result: 32 per cent correctly classified as to provenance.
Main discriminators: cutting angle, thickness, length, weight.
(Note: the 121 non-quartz Bondi points from BOB/1 were allocated as follows:

SH/1 — 20 (17%)
BOB/1 — 17 (14%)
MR/1 — 28 (23%)
M/1 — 11 (9%)
YC/1 — 35 (29%)
BL/1 — 10 (8%)

The large sample from BOB/1 and the spread of the tools into other groups during the analysis explains the drop in percentage when BOB/1 is included, i.e. from 46 per cent to 32 per cent.)

The final two runs included all eight sites previously analysed and also incorporated a series of other eastern New South Wales sites, viz., Capertee Nos. 1,2,3, and 4; Lapstone Creek; Stockton's Blue Mountains sites; Shaws Creek; and the Singleton surface collections of McCarthy and Davidson. A total of 1242 Bondi points were analysed. This additional data was kindly supplied by Ian Johnson.

(ix) *All non-quartz tools; all sites (as above)*
Variables: all attributes used.
Result: 14 per cent correctly classified as to provenance.
Main discriminators: Weight, length, cutting angle.

(x) *All non-quartz tools; all sites (as above)*
Variables: all attributes used.
Result: 27 per cent correctly classified as to provenance.
(Note: The Hunter sites — SH/1, BOB/1, MR/1, M/1, YC/1, BL/1 — were formed into one group, WR/1 and LM/1 into another group, and the remaining New South Wales sites listed above were entered individually. The Hunter group showed 52 per cent internal consistency and the coastal group 58 per cent consistency.)

In Table 9 the basic data employed during this computer analysis are given in condensed form.

The upshot of this analysis is that in the Hunter region, at least, there are significant variations between sites in the attributes of the tools produced and these have persisted over a time span of several millenia, the most marked variation being between coastal and inland sites. The industry at Bobadeen (BOB/1), when the quartz component is excluded, is the most generalised of the whole series (see Run viii above). This may be a product of the size of the sample or of the greater time-span of the site, as compared with the Hunter occupation period. Alternatively, it may be a difference of tradition between the western slopes and the eastern river valleys. The coastal craftsmen certainly appear to have produced consistently well-shaped and usually longer backed blades than those of the inland groups. Whether this was deliberate (being perhaps connected with shell-fish gathering activities), or whether it is a mechanical product of the high quality of the Merewether chert which predominates in coastal collections, can only be determined when considerably more archaeological work has been carried out in the area.

TABLE 9. BONDI POINTS: COMPARATIVE STATISTICS ALL SITES

| | | NON-QUARTZ | | | QUARTZ | | |
|---|---|---|---|---|---|---|---|
| Attribute | Site | N | Mean | Std Dev. | N | Mean | Std Dev. |
| Length (cm) | SH/1 | 58 | 2.51 | .724 | 0 | | |
| | BOB/1 | 121 | 2.19 | .725 | 76 | 1.63 | .346 |
| | MR/1 | 33 | 2.07 | .414 | 4 | 1.33 | .222 |
| | M/1 | 27 | 2.28 | .613 | 1 | 2.00 | |
| | YC/1 | 43 | 2.02 | .460 | 4 | 1.68 | .299 |
| | BL/1 | 32 | 1.92 | .503 | 7 | 1.47 | .150 |
| | WR/1 | 49 | 2.70 | .648 | 0 | | |
| | LM/1 | 69 | 2.86 | .867 | 0 | | |

**TABLE 9. Cont.**

| | | NON-QUARTZ | | | QUARTZ | | |
|---|---|---|---|---|---|---|---|
| Attribute | Site | N | Mean | Std Dev. | N | Mean | Std Dev. |
| Breadth (cm) | SH/1 | 58 | 0.74 | .190 | 0 | | |
| | BOB/1 | 121 | 0.73 | .174 | 76 | 0.71 | .165 |
| | MR/1 | 33 | 0.74 | .194 | 4 | 0.70 | .216 |
| | M/1 | 27 | 0.75 | .148 | 1 | 0.80 | |
| | YC/1 | 43 | 0.74 | .183 | 4 | 0.68 | .050 |
| | BL/1 | 32 | 0.73 | .309 | 7 | 0.71 | .090 |
| | WR/1 | 49 | 0.86 | .206 | 0 | | |
| | LM/1 | 69 | 0.75 | .235 | 0 | | |
| Thickness (cm) | SH/1 | 58 | 0.31 | .148 | 0 | | |
| | BOB/1 | 121 | 0.37 | .127 | 76 | 0.38 | .106 |
| | MR/1 | 33 | 0.33 | .110 | 4 | 0.35 | .058 |
| | M/1 | 27 | 0.39 | .138 | 1 | 0.50 | |
| | YC/1 | 43 | 0.40 | .176 | 4 | 0.45 | .058 |
| | BL/1 | 32 | 0.36 | .084 | 7 | 0.37 | .095 |
| | WR/1 | 49 | 0.46 | .141 | 0 | | |
| | LM/1 | 69 | 0.47 | .215 | 0 | | |
| Weight (gm) | SH/1 | 58 | 0.68 | .548 | 0 | | |
| | BOB/1 | 121 | 0.65 | .508 | 76 | 0.48 | .271 |
| | MR/1 | 33 | 0.45 | .200 | 4 | 0.28 | .150 |
| | M/1 | 27 | 0.66 | .560 | 1 | 0.80 | |
| | YC/1 | 43 | 0.70 | .543 | 4 | 0.58 | .096 |
| | BL/1 | 32 | 0.42 | .282 | 7 | 0.30 | .129 |
| | WR/1 | 49 | 0.71 | .430 | 0 | | |
| | LM/1 | 69 | 0.81 | .610 | 0 | | |
| Chord Angle (°) | SH/1 | 58 | 36.4 | 10.3 | 0 | | |
| | BOB/1 | 121 | 44.3 | 11.5 | 76 | 43.6 | 11.6 |
| | MR/1 | 33 | 49.5 | 13.1 | 4 | 64.0 | 8.8 |
| | M/1 | 27 | 39.7 | 7.3 | 1 | 50.0 | |
| | YC/1 | 43 | 39.9 | 12.1 | 4 | 48.0 | 10.7 |
| | BL/1 | 32 | 45.8 | 10.8 | 7 | 43.3 | 11.9 |
| | WR/1 | 49 | 45.3 | 11.1 | 0 | | |
| | LM/1 | 69 | 58.3 | 10.1 | 0 | | |
| L/B Ratio | SH/1 | 58 | 3.5 | 0.9 | 0 | | |
| | BOB/1 | 121 | 3.0 | 0.8 | 76 | 2.3 | 0.5 |
| | MR/1 | 33 | 2.9 | 0.8 | 4 | 2.0 | 0.5 |
| | M/1 | 27 | 3.1 | 0.7 | 1 | 2.5 | |
| | YC/1 | 43 | 2.8 | 0.8 | 4 | 2.5 | 0.6 |
| | BL/1 | 32 | 2.8 | 0.7 | 7 | 2.1 | 0.4 |
| | WR/1 | 49 | 3.3 | 0.9 | 0 | | |
| | LM/1 | 69 | 4.3 | 3.1 | 0 | | |

## DISCUSSION AND CONCLUSIONS

A number of problems and anomalies in the evidence from the Hunter region require further elucidation. In this section the most important of these will be discussed and some tentative conclusions reached. These may be supported, modified, or disproved when further work is undertaken in the area, particularly in the estuarine parts of the river valley.

Firstly, then, the comparative lateness of the basal dates of all the occupation sites excavated in the Hunter Valley itself and its immediate tributaries: these are remarkably consistent, particularly if the amended date for BL/1 is accepted. Since all the sites excavated were rock shelters (no open sites having been discovered), it could be argued that the rock overhangs of the region have only existed for the 2-3000 years they have been occupied. However, this seems most unlikely, since rock shelters in the country bordering the Hunter Valley (e.g. Bobadeen, Macdonald River, Capertee, Noola) have certainly been occupied for periods varying from 5000 to 10,000 years. It is scarcely conceivable that all the Hunter shelters should differ so markedly in their life-span from neighbouring overhangs in similar conglomerate sandstones and similar situations. In the light of present evidence, therefore, it has to be assumed that Aboriginal occupation of the upper and middle valley itself did not commence until about 3000 BP.

One possible reason for this has already been mentioned: that there was a late survival in the lower Hunter Valley of the formerly extensive rainforest, which still exists in a number of pockets in the central coast region, and that this provided an effective barrier to occupation of the middle Hunter from the coast.

An alternative hypothesis, which would accord with Bowdler's (1977) model for Aboriginal occupation of the Australian continent, is that the occupants of the continental shelf, moved back by the rising of the sea levels until about 6500 BP, were still so sparse that there was no pressure upon them to leave the coastal and estuarine zones to whose ecology they were perfectly adapted. The dating of occupation sites on the north coast (McBryde, 1965, 1966, 1974) and south of Sydney (Megaw, 1968, 1974), as well as the Macdonald River site (MR/1), would seem to fit this pattern. A burial and occupation site at Swansea Heads, excavated by Dyall but not yet published, has a basal date of 7500 BP (L. K. Dyall, pers. comm. 1978). The other aspect of Bowdler's model, that when Aboriginal coastal groups were eventually forced to move inland, they did so initially up the major river systems, would also seem to be endorsed by the Hunter evidence, if one assumes that occupation of the inland slopes of the Divide was made by groups moving eastward from the Darling-Murray river systems.

In the light of present evidence it would seem that the existing central coastline of New South Wales was not reached until between 8000 and 5000 BP by groups moving back from the continental shelf, whereas the western slopes of the Divide had already been occupied from inland at least as early as 10,000 BP. It is possible that the Divide itself and the rugged country to the eastward were left as a sort of no-man's land until tentative contact between the two waves of occupation was established, possibly at about the time of the start of the Bondaian. The south coast of New South Wales (and presumably the Victorian coast also) had been reached even earlier, by 20,000 BP at the latest (Lampert, 1971). Stockton's Blue Mountains sites (Stockton & Holland, 1974), some of which appear to date back as far as 20,000 BP, may seem anomalous in this model. However, Ann Ross (1976) in her reconstruction of the ethnographic picture in the Sydney-Blue Mountains area found a similar situation to that indicated here for the Hunter Valley; that is, the coastal and estuarine people had little or no contact with the groups inland on the Hawkesbury system and in the mountains. It is possible, therefore, that there was penetration into the area of the Divide from the Darling-Murray system in a period much earlier than the coastal occupation by people moved back from the continental shelf by the post-Pleistocene rise in sea-level. Alternatively it may be found that the Blue Mountains dates are not supported when further archaeological work is carried out in the area.

The second matter which this survey aimed to elucidate was the prehistoric relationship between the people of the estuarine and freshwater reaches of the Hunter River system. The only ethnographic hint that we have about contact between the coast and the middle Hunter is Threlkeld's remark (1974:42) that the coastal Aborigines in the Newcastle area traded Xanthorrhoea stems (for spearshafts) with the inland people in exchange for possum-fur belts. However, even this contact may not have been via the Hunter Valley itself, but by traditional tracks along the tops of the scarps to the south, where the cover is light sclerophyll and movement is comparatively easy. This solitary reference to trade between the coast and inland does not, therefore, automatically invalidate the suggestion that the valley was blocked by impenetrable rainforest until quite recently. In any case, the river itself would probably have been navigable.

So far as the archaeological record is concerned, the material used for flaking in the two areas differs completely, the middle Hunter tools being almost entirely manufactured from local red to yellow cherts and quartzites, whereas the estuarine and coastal industries employed Merewether (or "Nobby's") white to grey chert almost exclusively. This applies both to the small-tool component and to the heavy core and flake artifacts found in surface collections in both areas. A similar dichotomy may also be present in the differences between the backed blades from the coastal surface collections and the inland excavated material, as detected in the computer analysis of Bondi points. However, the variation in size and weight between Dyall's sand-dune collections and the backed blades excavated in the middle Hunter sites could also be explained as a factor either of mechanical sorting in the shifting dune environment or of unintentional selection on the part of the collector. Nevertheless, the Williamtown collections were total collections made during a considerable number of visits and the material was deliberately taken from a surface with a compacted layer immediately underlying it. The Swansea material was not collected under quite such tightly-controlled conditions (Dyall, pers. comm. 1978).

The absence of the large core and flake component from all excavated Hunter sites argues for this having predated the microlithic complex in the middle Hunter and adjoining areas. The time-span and sequence of tool types in the Hunter estuary cannot be elucidated in the absence of an excavated sequence from the Hunter mouth.

From the sparse ethnographic record it would seem that the contacts of the estuarine Aborigines were strongly oriented to north and south, the Awabagal having frequent intercourse with the Gaddhang, who in turn extended to the northern fringes of Port Stephens, where they were in contact with the Birbai of the Manning estuary. Regarding the contacts between the Wonarua and their neighbours to the west and south, rather more may be said. Enright informed McCarthy (pers. comm., see McCarthy and Davidson, 1943: 228) that the Wonarua were a "horde" of the inland Gamilaroi. Presumably this information originated from Gaddhang remnants, since Enright's contacts were mainly confined to the coastal groups (and it is doubtful whether any Wonarua had survived into his period). Even so, the information is of some significance, since it indicates that the Wonarua were oriented more to the inland than the coast. The contacts, both friendly and hostile, between the Wonarua and the Gamilaroi via the lower reaches of the Goulburn were described in Part I of this survey, where it was suggested that Gamilaroi raiding into the middle Hunter may have been a historic relic of Wonarua intrusion up the valley from the coast. In the light of the fresh evidence presented here, it seems more likely that the Wonarua may have been descendants of a group which hived off from the Gamilaroi and moved into the upper valley from the west only a few thousand years ago. The fact that the Gamilaroi raiding appears to have been mainly to obtain wives could be taken to support this theory.

Contacts between the Wonarua and the Darginung to the south, along the Boree Track, seem to have been mainly for joint ceremonials and trade; this is reflected in the rock art of the region between the Hunter and the Hawkesbury and also in the presence of Hunter Valley cherts and quartzites in the tools and waste excavated at MR/1 on the Macdonald River. The apparent intensification of occupation in sites at both ends of the Boree Track about 2000 BP has already been mentioned. This may be a product of the late occupation of the Hunter Valley. If, as the survey seems to imply, Aboriginal occupation of the valley began only about 3000 years BP, then contact between the Wonarua and the Darginung may not have been established until towards the end of the third millenium BP, but may then have grown rapidly. The apparent presence of Hunter Valley cherts at MR/1 from at least 5000 BP would seem at first sight to imply trade between the Hunter and the Hawkesbury. However, in view of the consistency of the dating of the Hunter-Wollombi sites at c.3000 BP, it seems more likely that the Hawkesbury Valley people were periodically visiting the then unoccupied middle Hunter via the Wollombi and Milbrodale routes in order to obtain the raw material for themselves. It is just possible that the anomalous Milbrodale paintings are a relic of this period, since they are at precisely the point where several natural routes from the Hawkesbury emerge into the Hunter Valley itself. After occupation of the middle Hunter by the ancestors of the Wonarua about 3000 BP, probably the material was obtained by exchange in the vicinity of Wollombi.

The presence of Merewether chert also in the MR/1 deposits over a time span of more than 5000 years would seem to imply that it was obtained via the Hawkesbury River and Broken Bay from the Awabagal, rather than via the middle Hunter. The presence of black cherts, possibly from the Wagonga beds of the south coast, must have resulted from intercourse between the Darginung and the people of the Port Jackson region. The Darginung, in fact, appear to have been the middlemen in a far-reaching network of distribution of lithic raw materials and it may be assumed that they were also distributors of other more perishable goods which have vanished from the archaeological record. The Darginung territory contains some of the most outstanding rock art in the whole central coast region, so it may also be that they were catalysts in the spread of myth, ritual, and visual art. The cave paintings in the Wonarua area, on the other hand (with the sole exception of the Milbrodale site), are closely allied to those on the western side of the Divide, which is a further argument for their having been a sub-group of the Gamilaroi.

The picture that emerges from all of this is of a clear division between the coastal and inland tribes in the Hunter Valley. Whether the causes of this were geographical or historical cannot yet be stated definitely. However, the situation does appear to conform to Bowdler's model and it begins to seem as though the east coast may have been the last region to have been occupied in the gradual spread of the Aboriginal colonists from the north-west to the south-east of the Australian continent.

Although some of the dates from the east coast appear to be earlier than what is currently taken to be the climax of the post-Pleistocene marine transgression (i.e. about 6500 BP), the occupation sites so dated may well have been intermittently visited by groups from the continental shelf. Such visits may have been to exploit particular food zones or to obtain particular types of stone or other raw material for implement-making. Nevertheless, the fact that all dates obtained so far from the existing coastline show a distinct cline from south to north would seem to indicate a similar differential in the time of occupation of the continental shelf.

## ACKNOWLEDGEMENTS

Without the continuing support of the Australian Museum Trustees, its former Director, Dr F. H. Talbot, and his successor, Dr D. J. G. Griffin, this survey could not have been carried out. A series of small grants from the Australian Institute of Aboriginal Studies covered the basic costs of fieldwork; and the sympathetic interest of its former Principal, Mr F. D. McCarthy, and his successor, Dr P. J. Ucko,, gave encouragement on many occasions. A personal grant from Mr P. H. Pigott made possible the employment of Val Attenbrow as a research assistant during the preparation of this report.

The expert assistance of the following was much appreciated: Professor D. Branagan, Professor L. K. Dyall, Dr Richard Gillespie, David Hain, Ian Johnson, and Henry Polach.

For the second half of the survey members of the excavating parties, who always worked willingly and cheerfully, were as follows: Charles Vale, Chris Irwin, Gwen Moore, Gail Anderson, Robert, Beverley and James Ingram, Dr S. M. Bard, Tessa Corkill, and Carol Powell. Assistance in sorting, analysing, etc. was given by Dr S. M. Bard, Tessa Corkill, Carol Powell, Val Attenbrow, and Ann Ross.

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Manuscript accepted for publication 12th July, 1979.

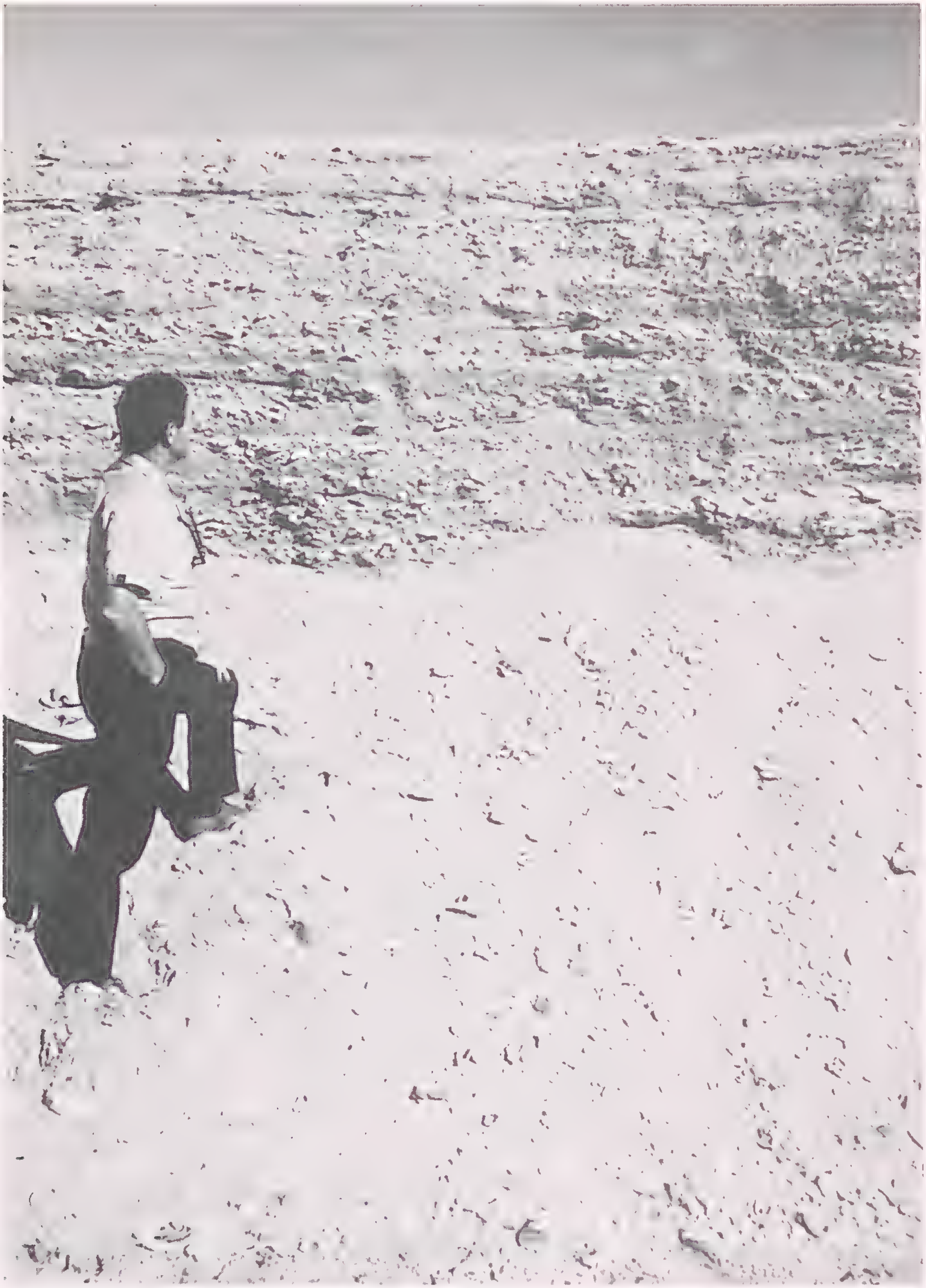


Fig. 5. Shell heap on Ash Island, Hunter estuary. When this photograph was taken on 12/3/70 this last remnant of a formerly huge mass of shells was in process of being bulldozed.

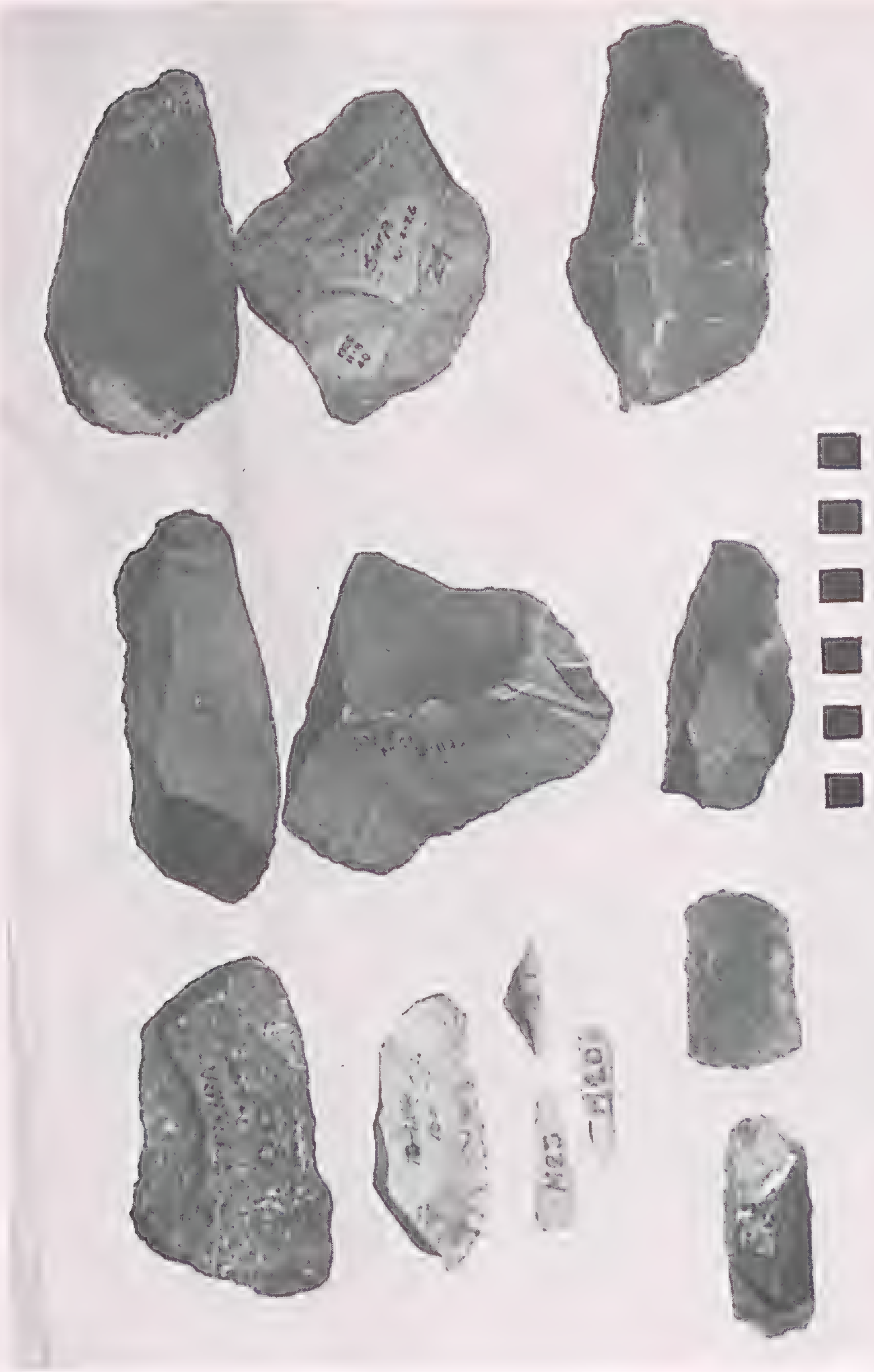


Fig. 6. Artifacts from the Cooksey collection in the Museum of Mankind (British Museum). These are all from Tirrikiba and Mayfield, inner suburbs of Newcastle. (Scale in cm.)

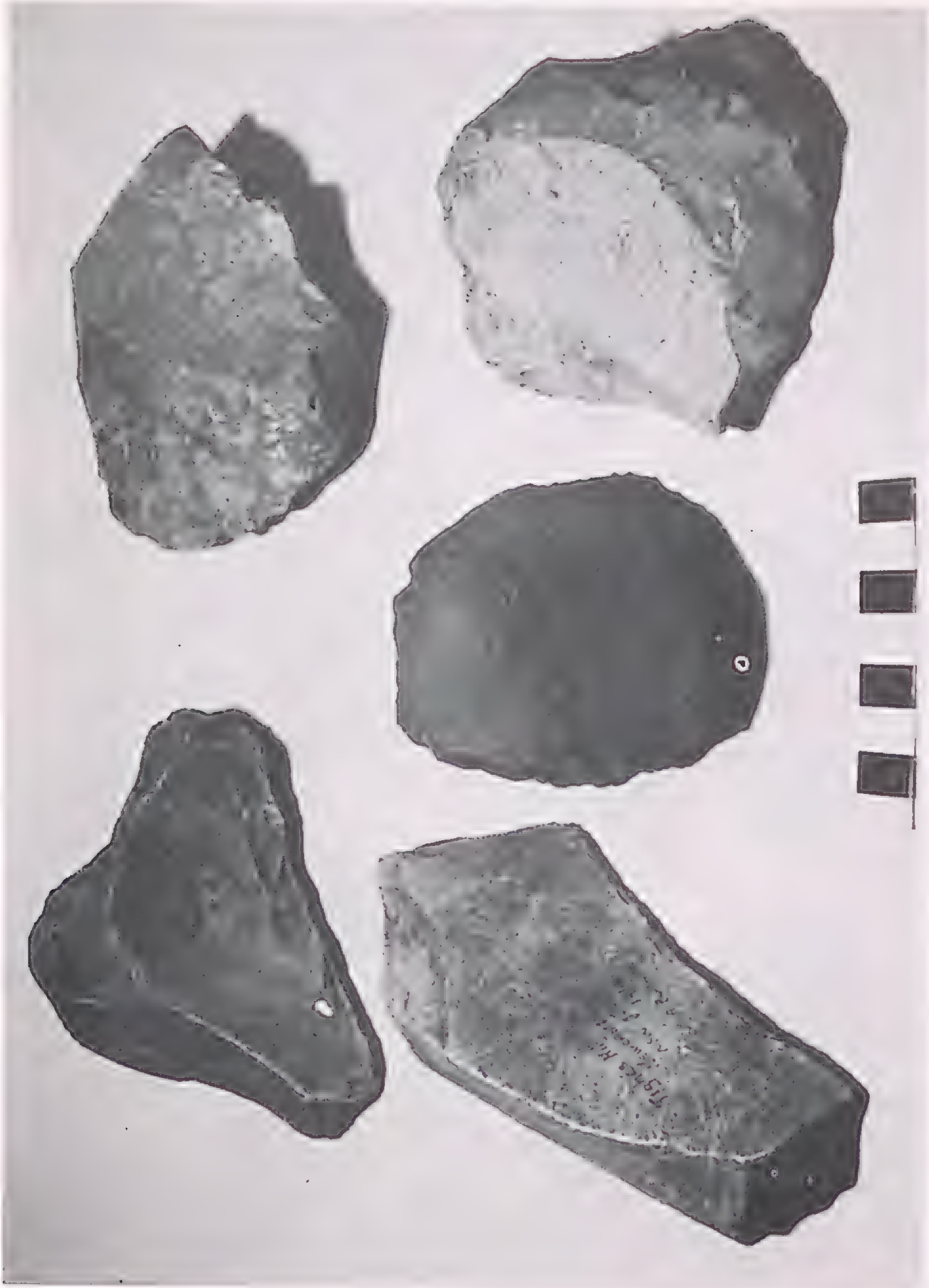


Fig. 7a. Artifacts from the Gwynne collection in the Australian Museum. All come from Tighe's Hill, an inner suburb of Newcastle. Illustrated here are examples of the large tool component. (Scale in cm.)

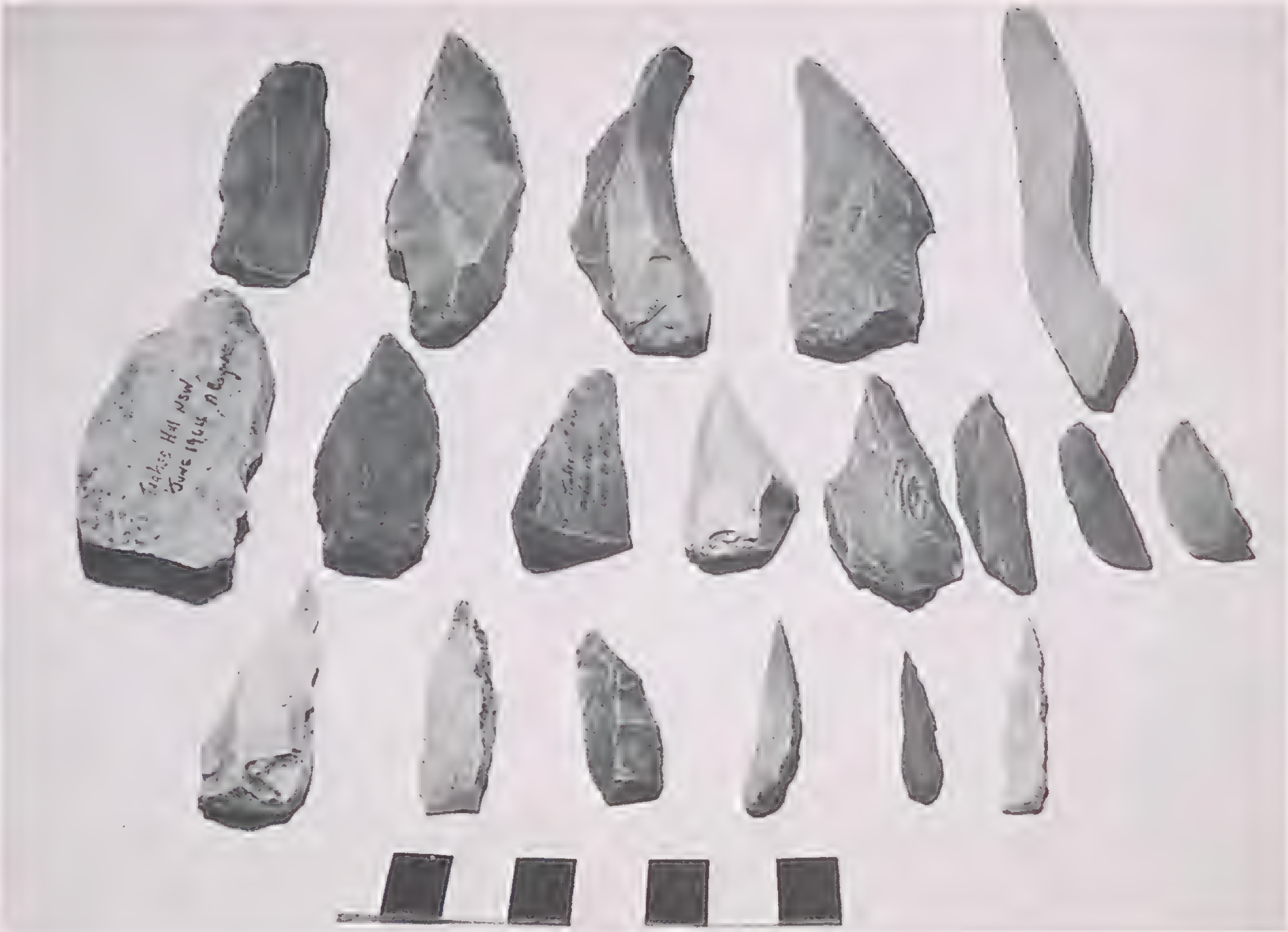


Fig. 7b. Artifacts from the Gwynne collection. These are a representative selection from the small tool component. (Scale in cm.)

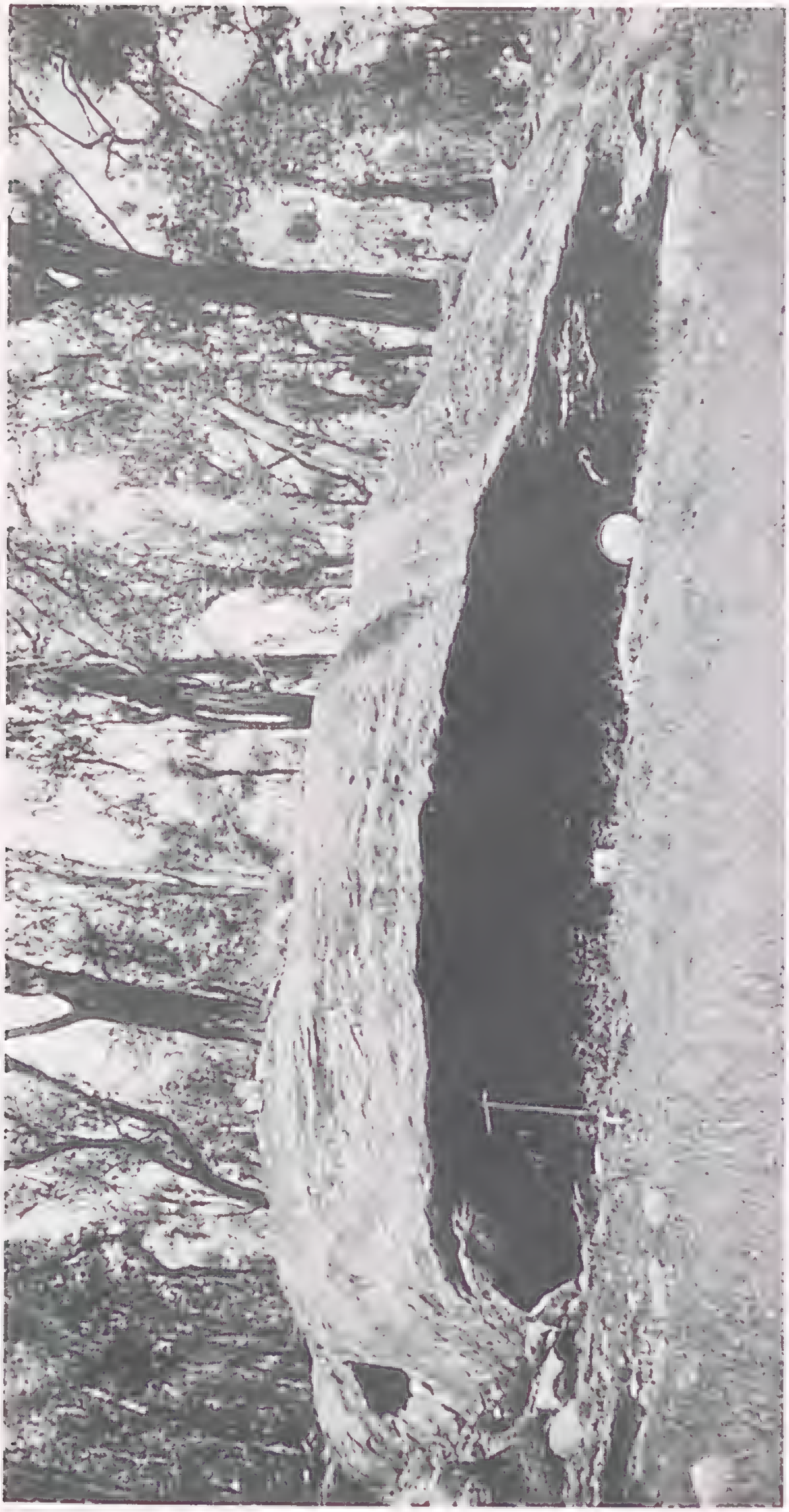


Fig. 8a. Site BL/1: general view of shelter. Big L Creek is about 100 yards down the slope in front of the shelter.

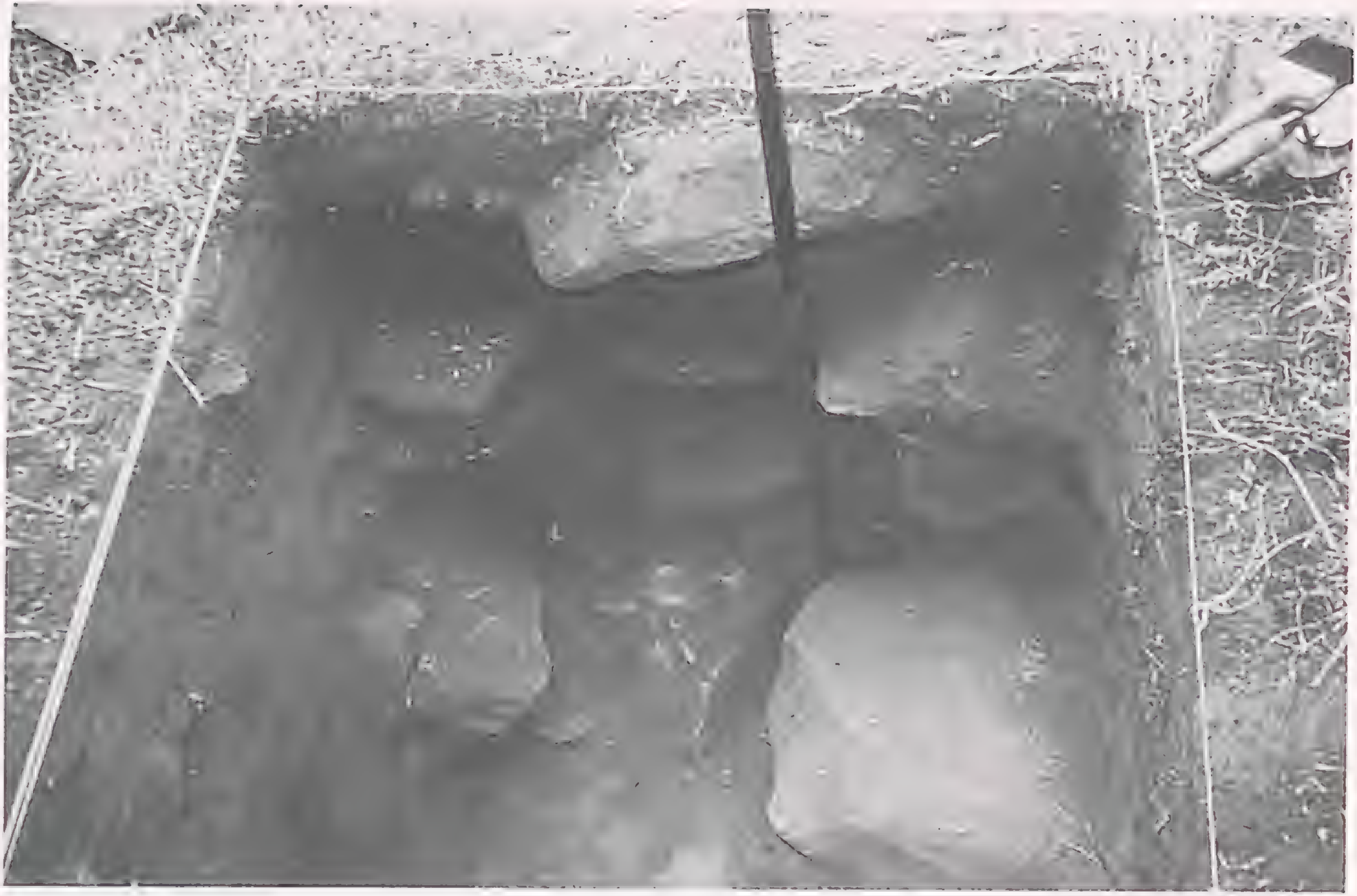


Fig. 8b. Site BL/1 excavation: end of Square A, the only square excavated, at 30 inches depth. (Ranging pole in feet.)

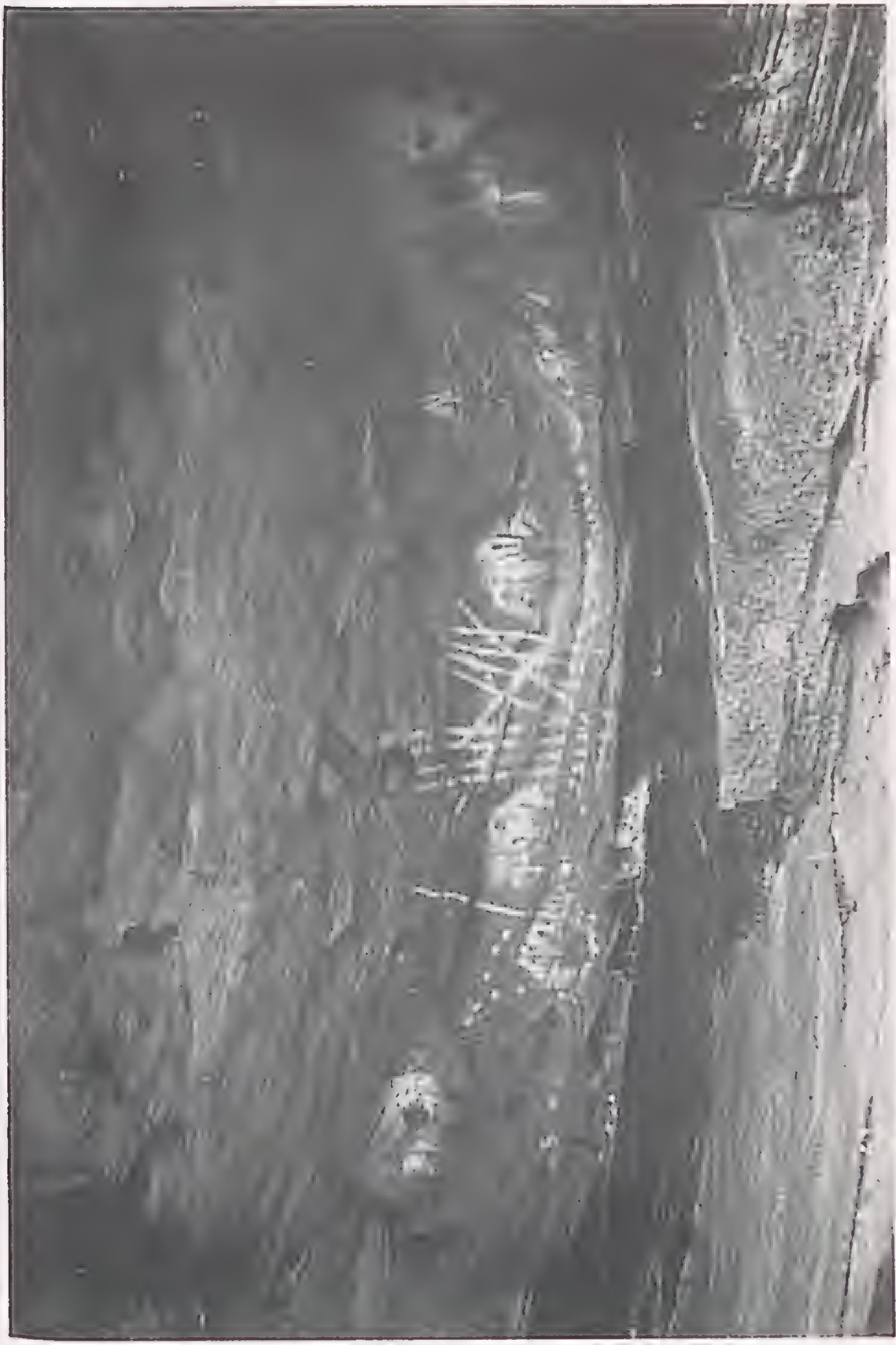


Fig. 9a & b. Site BL/1: paintings. At this site the stencils, radiate signs and tally marks appear to have been carefully placed and superimpositions are rare.

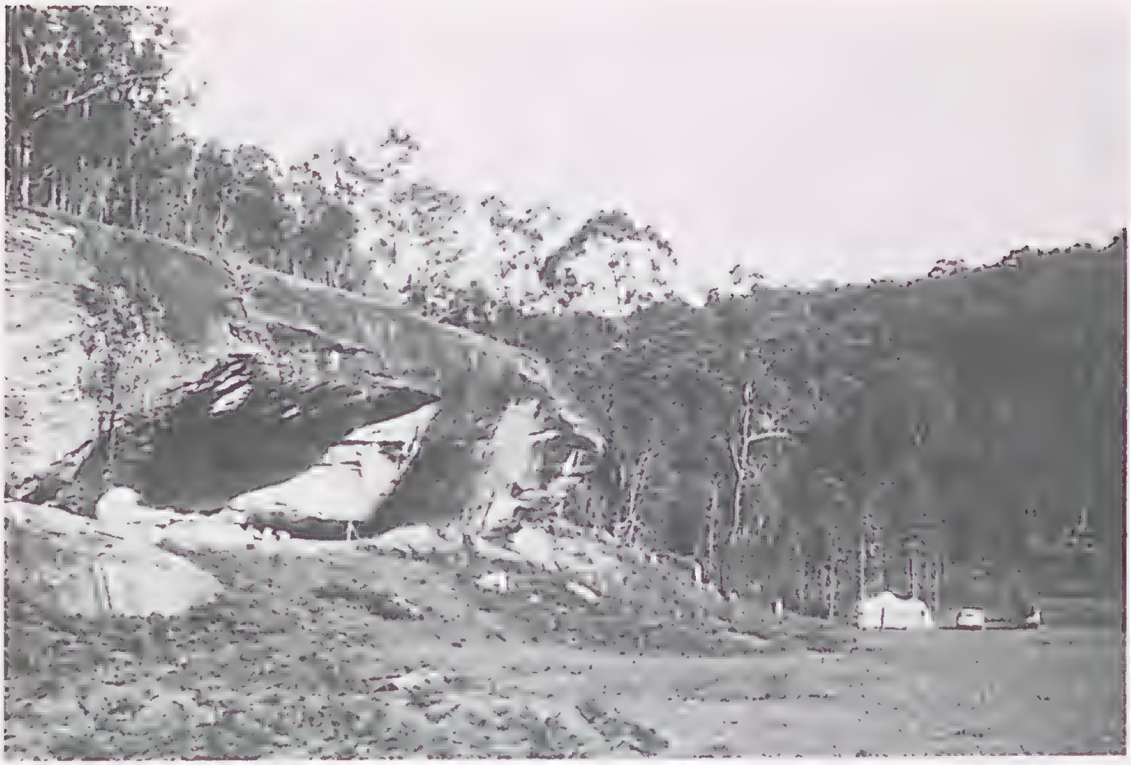


Fig. 10. Site YC/1: general view. Yango Creek is about 200 yards from the shelter across a level valley floor.

Fig. 11. Site YC/1 excavation: Square DD, level 11. The apparent changes in the soil profile are due to drying out of the section during excavation. (Ranging pole in feet.)

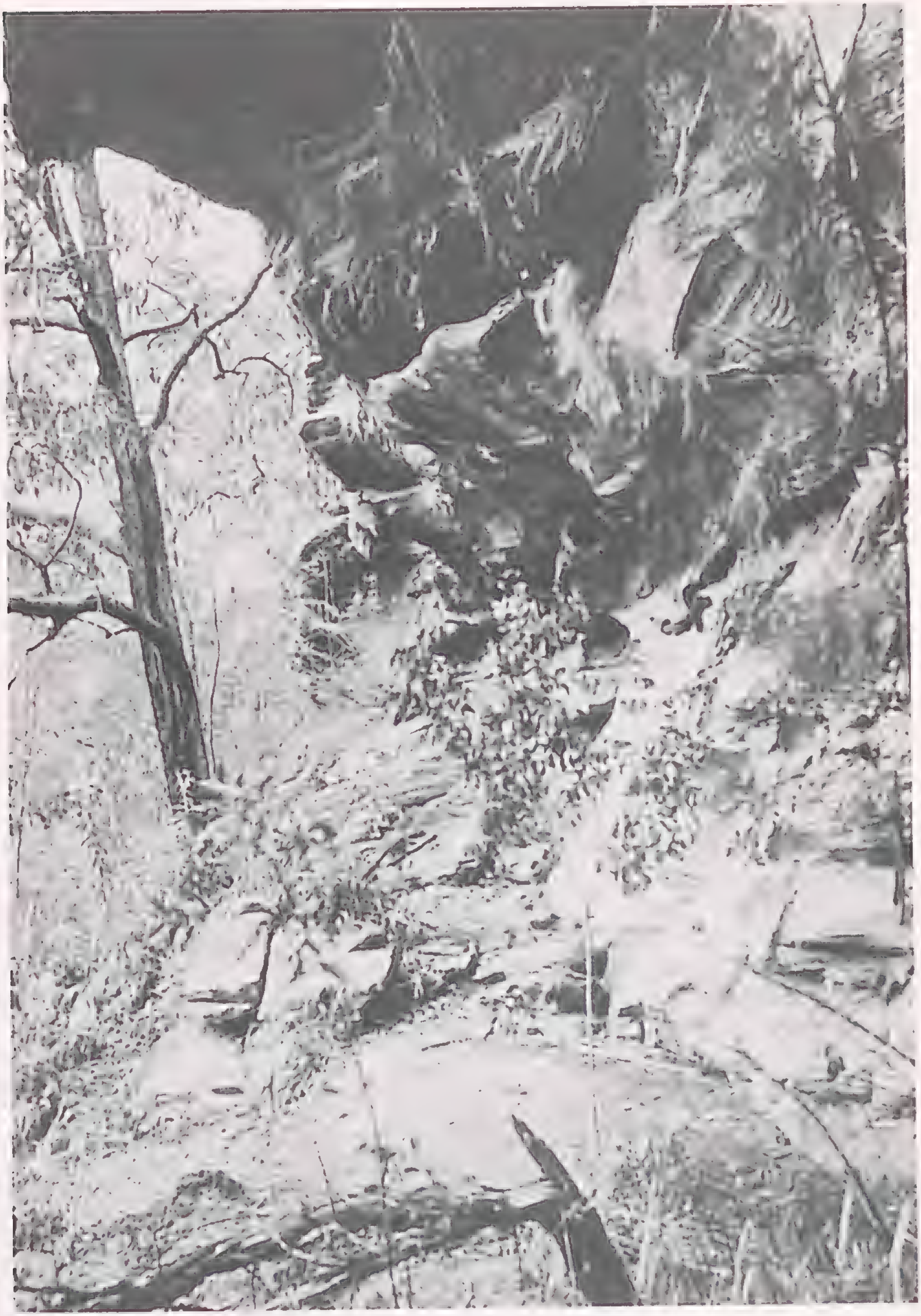


Fig. 12. Site MR/1: general view of shelter before excavation, looking east. The section excavated was in the immediate foreground.

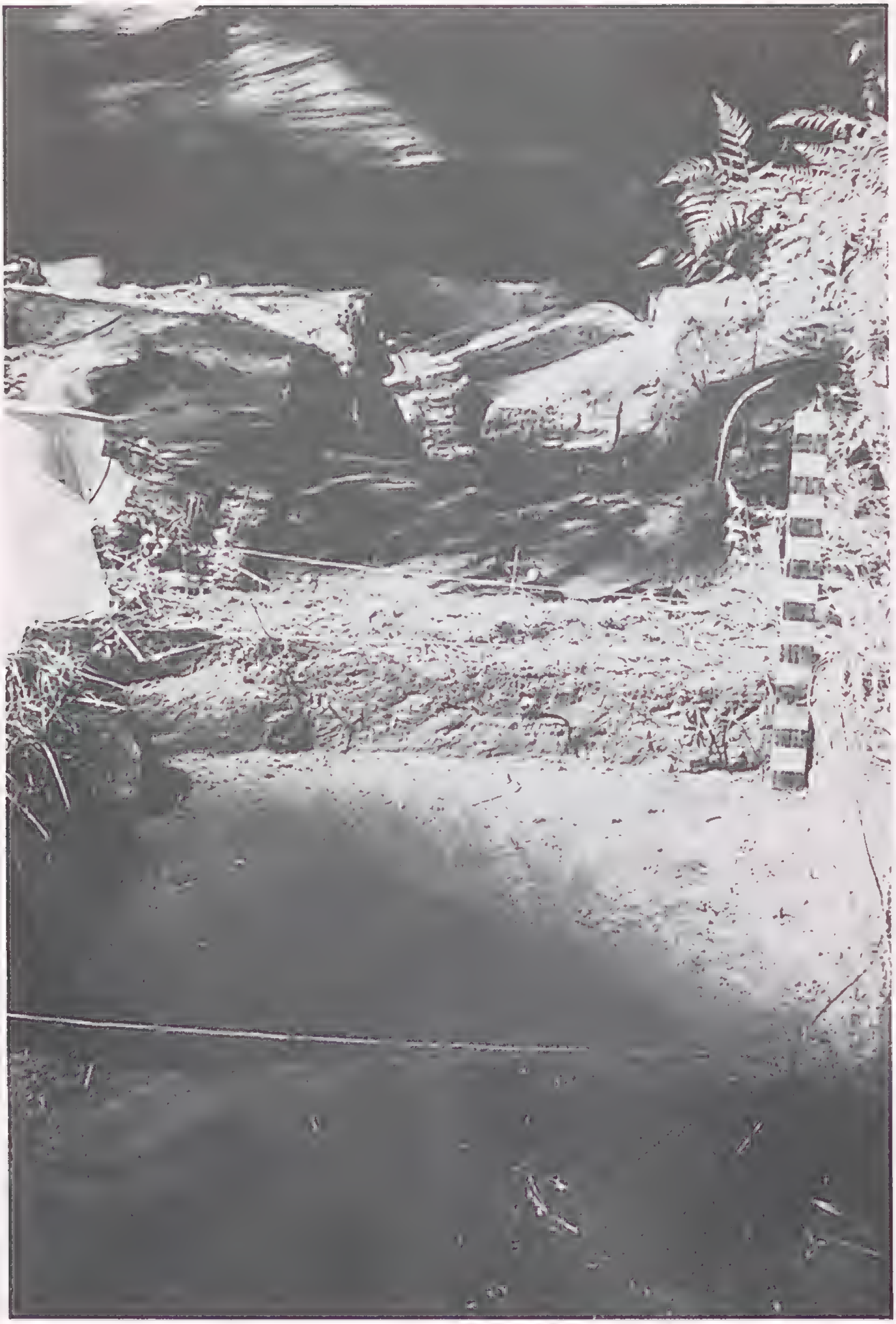


Fig. 13a. Site MR/1 excavation: looking along the datum line towards the back wall of the shelter. Included are Squares B, C, and D. (Scale in inches.)

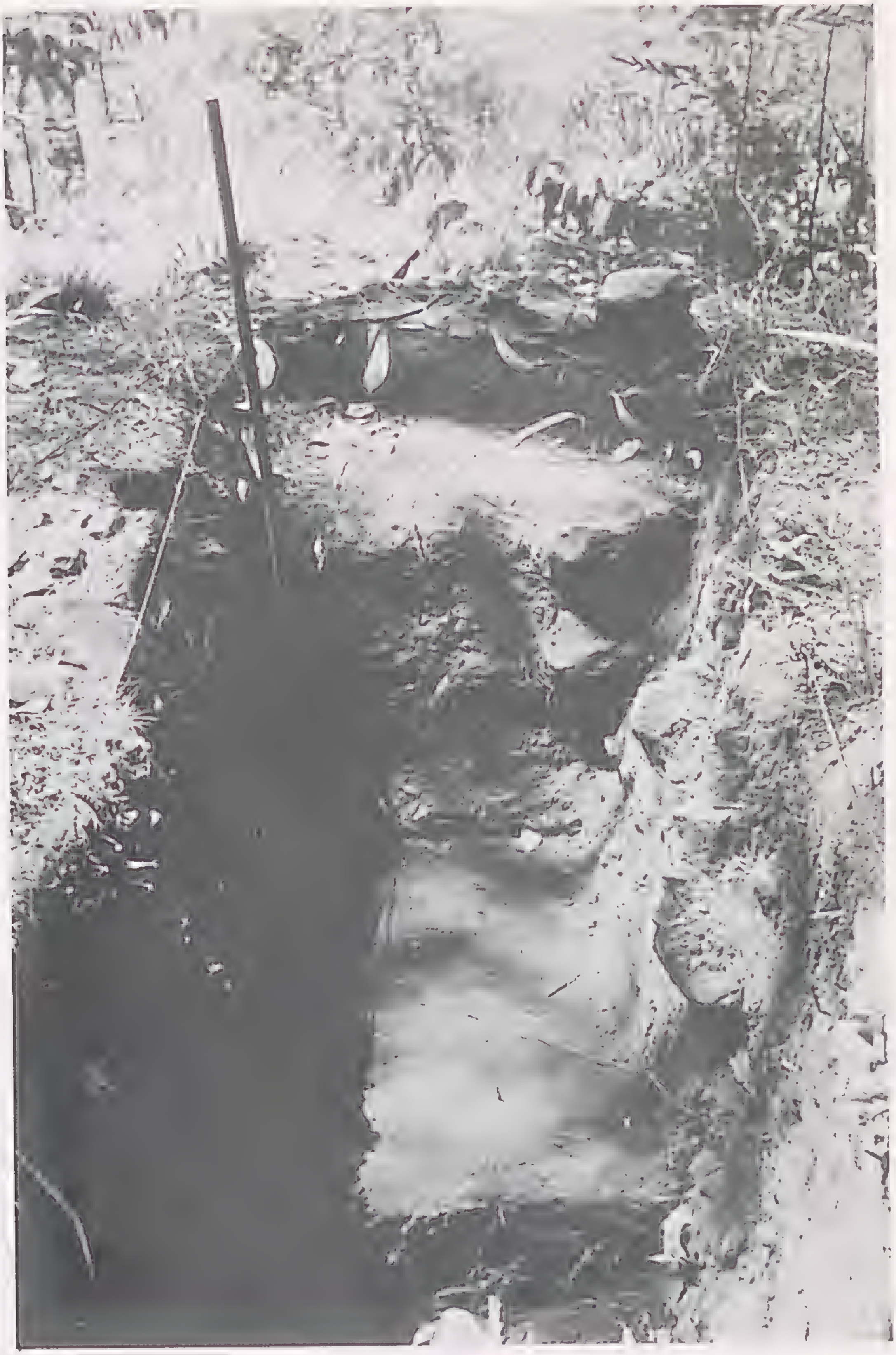


Fig. 13b. Site MR/1 excavation: looking along the datum line towards the talus slope. Squares shown are AA, BB, and CC. The Macdonald River is about 200 feet below, down a very steep drop.

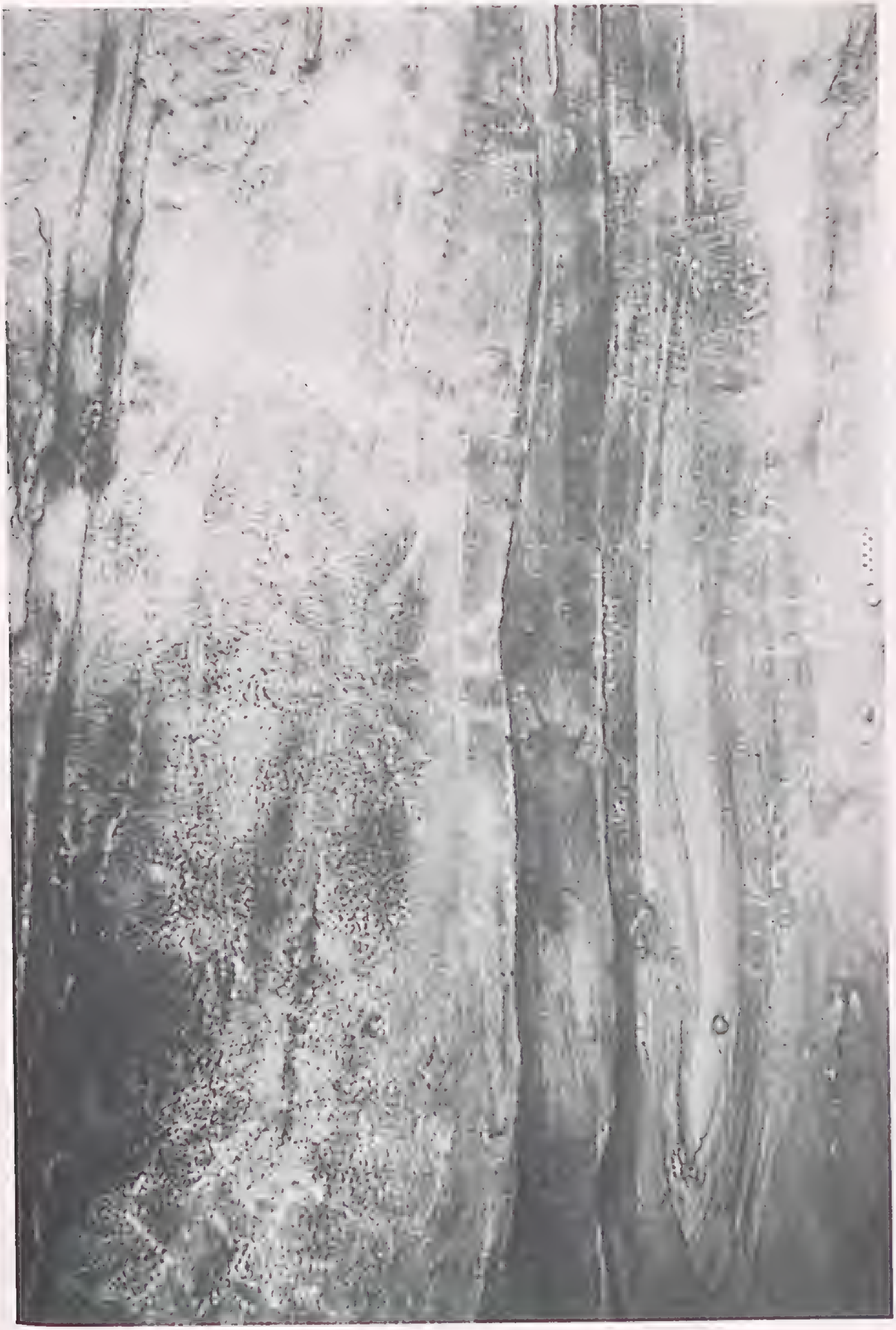
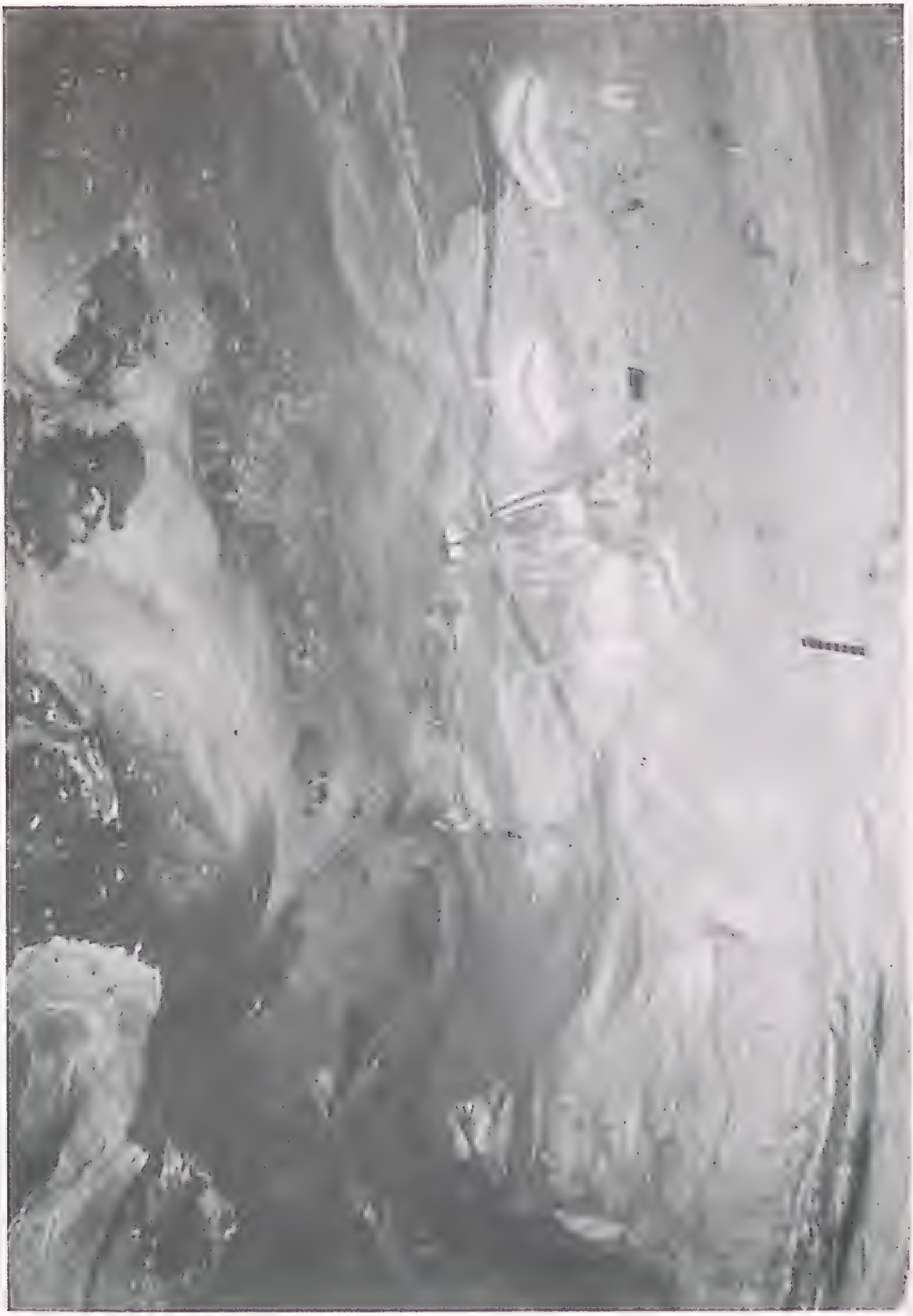


Fig. 14a & b. Site MR/2 paintings: note radiate symbol and small dancing figures in black and white line. (Scale in cm.)



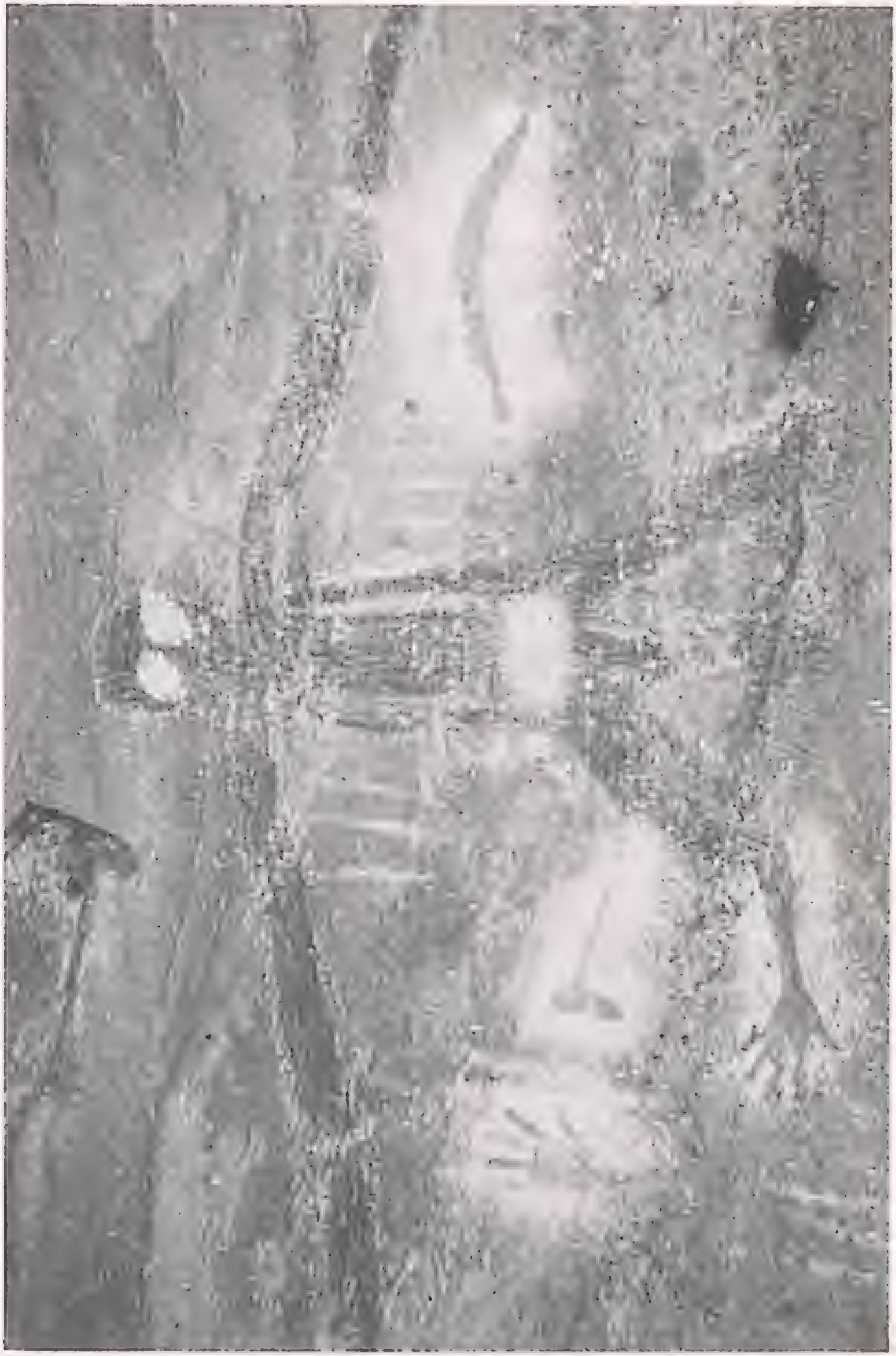


Fig. 15a & b. Milbrodale: paintings. The arms of the "culture hero" extend along the rock face for 18 feet. (Scale in inches.)

# GUIDE TO AUTHORS

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The manuscript — including tables, headings, indices, legends to figures, and literature cited — must be clearly and neatly typewritten, double-spaced, on one side of bond or other good quality paper, and with 3 cm margins all round. Pages should be numbered consecutively. Tables and legends to illustrations should be on separate pages at the end of the manuscript. The entire manuscript should be securely fastened together.

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Papers should be arranged as follows:

(i) The title, which should be concise and specific. The higher classification of the group dealt with should be indicated in the title of zoological papers; in palaeontological papers the position of a local formation in the world scheme should be indicated.

(ii) The author's name and professional address.

(iii) A summary not exceeding either 3 per cent of the text or 200 words and intelligible to the reader without reference to the main text.

(iv) A list of contents may be included if the paper is very long.

(v) Introduction.

(vi) The main text of the paper.

(vii) Acknowledgements.

(viii) References (see below).

(ix) Index (in the case of very long papers).

The approximate position of tables and figures should be indicated in pencil at the left-hand margin.

Only the names of genera and species should be underlined. Unless indicated elsewhere in the text, or where nomenclature follows a generally accepted standard (which should be cited), the authority should be cited when any specific name is used for the first time.

In taxonomic papers the short form (taxon, author, date, page) should be used in synonymies and the full reference taken to the end of the paper. In synonymies a period and dash (—) should separate the name of the taxon and the name of the author except in the case of the reference to the original description. Where new species are described the location of the type material must be indicated and Article 73 and associated recommendations of the International Code of Zoological Nomenclature should be followed. Dichotomous keys with contrasting parts of couplets adjacent to each other are recommended. In these only the first part of the couplet should be numbered and the beginning of the second indicated with a dash at the left-hand margin. Keys must not use serially indented couplets. Papers not following this form of presentation will be returned to the authors.

### Tables

Tables should be typed on separate sheets and numbered in Arabic numerals. Headings should be

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# THE GALAXIID FISHES OF AUSTRALIA (PISCES: GALAXIIDAE)

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## INTRODUCTION

The family Galaxiidae comprises mostly small, scaleless fishes (to about 600 mm long, usually less than 250 mm) that are frequently benthic and cryptic in habit. Most species are elongate and fusiform, often with broad, somewhat depressed heads and thick fleshy fins. Some species are free-ranging in pools and lakes. These tend to have more membranous fins, are more slender in form, and are sometimes slightly compressed. Cryptic species usually have truncate to rounded caudal fins while the more open-living species may have forked tails.

The family is confined largely to the southern temperate zone, occurring in temperate and sub-tropical western and eastern Australia, Tasmania, Lord Howe Island, New Caledonia, New Zealand, the Chatham, Auckland and Campbell Islands, Chile, Patagonian Argentina, Tierra del Fuego, the Falkland Islands and the southern tip of South Africa. A species of *Galaxias* was described from India by Day (1888) but the identity of the fish has never been adequately established and *Galaxias indicus* Day (1888) is regarded as a *nomen dubium* by McDowall (1973a).

Diversity of galaxiid fishes is greatest in Australia with 20 species in three genera; there is one endemic species in the uplands of New Caledonia (McDowall, 1968a), and another widespread species at Lord Howe Island. Two genera and 13 species occur in New Zealand and its outlying islands (McDowall, 1970a, 1972a), four species in two genera in South America and the Falkland Islands (McDowall, 1971), and a single species in South Africa (McDowall, 1973b). Most species are endemic to one of the major geographical areas within this range, although *G. maculatus* (Jenyns) is known from Western Australia, eastern Australia (from southern Queensland south and west to South Australia), Tasmania, Lord Howe Island, New Zealand, the Chatham Islands, South America and the Falkland Islands. *G. brevipinnis* Günther occurs in eastern Australia, from central coastal New South Wales, south and east to South Australia, Tasmania, New Zealand, the Chatham, Auckland and Campbell Islands. *G. truttaceus* (Valenciennes) is found in Western Australia, eastern Australia (Victoria), and Tasmania.

Most galaxiid species are confined to fresh waters but several are known to be diadromous with the larval, post-larval and juvenile phases occurring in the sea (McDowall et al., 1975). One species, *G. maculatus,* is known to spawn in tidal, estuarine waters (McDowall, 1968b) but all others are believed to spawn in fresh water, movement to sea in diadromous species probably taking place soon after hatching in fresh water (e.g. Ots and Eldon, 1975). Very little is known about the natural history of galaxiid fishes, except for *G. maculatus* which has been the subject of intensive study — it has considerable commercial importance in New Zealand and is taken in small fisheries in Tasmania and Chile (McDowall, 1968b; Scott, 1938; Campos, 1970, 1973, 1974). Other species have also been studied in less detail. Benzie (1968a) examined the life history of a New Zealand species, *G. vulgaris* Stokell; Cadwallader (1975a, b, 1977) added to knowledge of this species and also examined aspects of the natural history of *Neochanna burrowsius* (Phillipps), another New Zealand form (Cadwallader, 1975c). Hopkins (1971) described the life history of *G. divergens* Stokell (New Zealand), and Eldon (1968, 1971, 1978) discussed varied aspects of the natural history of *Neochanna apoda* Günther (New

Zealand). Campos (1972b) described parts of the life history of the Chilean *Brachygalaxias bullocki* (Eigenmann).

Little work has been done on Australian species although Walford (1928, 1941, 1942) studied the life cycle of *G. olidus* Günther (identified as *G. coxii* Macleay) and Scott (1941) looked at aspects of the natural history of *G. truttaceus* in Tasmania. Pollard (1971-1974) in a long series of papers made an intensive study of the biology of a landlocked population of *G. maculatus* in Victoria, while Chessman and Williams (1975) studied salinity tolerance in this species. Berra (1973) studied home range in *G. olidus* Günther (referred to as *G. bongbong* Macleay), and Tilzey (1974, 1976) has reported on effects of trout invasion on populations of this species. Despite an apparently substantial series of publications on galaxiid fishes, little remains known about most species.

The family Galaxiidae constitutes a major proportion of the freshwater fish fauna of southern Australia, and is, by far, the largest family in cool and cold waters of the area. Although some galaxiids are present in Western Australia north of Perth, and in southern Queensland, greatest diversity and abundance occur in southern waters, particularly in Tasmania. Of the 20 species recognised in this revision 15 are present in Tasmania and 11 are restricted to the island. Western Australia has a small galaxiid fauna of five species, three endemic.

The systematics of galaxiid fishes have always been a problem; detailed and intensive studies of the Australian species have been few, and some have been redescribed repeatedly. Thus *G. maculatus* is known in the literature under 17 names in Australia alone and a further nine names in other parts of its range. *G. brevipinnis* has been described under seven names in Australia and a further eight in New Zealand. *G. olidus* has a total of eight synonyms in Australia. It is therefore not difficult to imagine the confusion that has developed. Misidentifications have been common and populations from a given area have been given a variety of names by various authors. The 20 Australian galaxiids recognised in this revision have a total of 58 names.

The family Galaxiidae was revised by Regan (1905). In this, the only comprehensive revision of the family ever attempted, 14 species were attributed to Australia of which only seven are recognised here. E.O.G. Scott began work on the Tasmanian galaxiid fauna in the 1930's, described several species as new, and revised the Tasmanian galaxiid fauna in 1936. He has continued to study and revise various parts of the fauna, describing new species and subspecies, or discussing variation and natural history of diverse galaxiid species (Scott, 1934-1974).

Whitley (1935, 1956a, b, 1964) published name lists and synopses based largely on knowledge of the literature. Stokell (1966) proposed some nomenclatural modifications that have generally been rejected by other workers for various reasons (McDowall, 1967a; Scott, 1968). On the whole the galaxiid species of mainland Australia have received scant attention, with only a few publications seeking to distinguish species belonging to particular states, e.g. Mack (1936) — Victoria; Whitley (1944) — Western Australia; Waite (1933), Scott (1962), Scott et al. (1974) — South Australia; McCulloch (1921) — New South Wales. Munro (1957) published a synopsis of the Australian species but his contribution is no more than a rather superficial literature assessment of the fauna introducing few nomenclatural changes, none of which is adequately documented.

The description in 1961 of a so-called scaled galaxiid — *Lepidogalaxias salamandroides* Mees — created much interest, but osteological studies have indicated that the fish is not a galaxiid (Frankenberg, 1969; McDowall, 1969; Rosen, 1974), and this strange little fish is not dealt with further here.

Frankenberg (1967) described two new species of *Galaxias* from the Lake Pedder region of Tasmania, species that became noticed when controversy developed over the modification and ultimate inundation of the lake to form a water storage reservoir. In a recent listing of Australian galaxiids Lake (1971) recognised 25 species of which only 13 are recognised here; he omitted to list two valid and previously described species, and had no knowledge of five species which were not then described (McDowall and Fulton, 1978a, b; Fulton, 1978a, b; McDowall, 1978a).

Andrews (1976) revised the Tasmanian galaxiid fauna, recognising ten species; all of these are recognised in the present study, although certain name changes are proposed. It is shown, in one instance, that Andrews' description is based on three distinct species — Andrews' *Paragalaxias shannonensis* Scott represents *P. dissimilis* (Regan) and two further, then undescribed species of *Paragalaxias.* Since the completion of Andrews' revision these two further species have been described (McDowall and Fulton, 1978a) and three additional galaxiids have also been discovered (Fulton, 1978a, b; McDowall and Fulton, 1978b).

Material examined from Western Australia revealed a new species belonging to the species group widely recognised in the literature as *"Brachygalaxias"*. The new genus *Galaxiella* was described for these species, and the new species from Western Australia described (McDowall, 1978a).

From the foregoing discussion it is clear that a comprehensive revision of the Australian Galaxiidae is long overdue, the Australian section of the family being the only part not subject to revision in recent times. As long ago as 1935, Whitley claimed (correctly), that systematics of Australian galaxiids were in "a parlous state", while Lake (1959:4) stated that there was "still some disagreement and confusion regarding some species" — a substantial under-statement. Later, Lake (1971:20) added "I do not believe that, even at the specific level, one can justify all species which have been described".

The present study therefore seeks to establish and redescribe the galaxiid species of Australia. The work has a dual origin. In the late 1960's Frankenberg wrote a Ph.D. thesis on galaxiid fishes (Frankenberg, 1969), in which a variety of problems related to their systematics and relationships was examined, including a partial resolution of the taxonomy of Australian members of the group. Of particular relevance to the present study, species groups were identified and diagnosed and nominal species in each group were analysed. The origin and evolution of species within each species group were explored, and informal taxonomic arrangements, based on these analyses, prepared. However, there were no formal synonymies or descriptions and no keys for identification or diagnoses. Frankenberg's work remains unpublished. McDowall was invited to spend a period at the Australian Museum, Sydney, under a grant from the Interim Council of the Australian Biological Resources Study, to resolve the taxonomy of Australian Galaxiidae. During tenure of this grant, a substantial amount of additional material was collected and examined by McDowall, extensive morphometric data on these fishes accumulated and much additional meristic data added to extensive data already available in Frankenberg's thesis. In addition six new species were identified. The present publication represents a synthesis of these two independent studies, and forms the logical sequel to McDowall's (1968a, 1970a, 1971, 1972, 1973a, b, c) studies of New Caledonian, New Zealand, South American and South African galaxiids.* It is restricted to a treatment of taxonomy; relationships of the species and their zoogeography will be discussed in subsequent papers.

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*The taxonomic arrangement reflects the opinions of the senior author and does not, in every case, coincide with those of the second author.

## MATERIAL EXAMINED

Prior to Frankenberg's study, galaxiid material in Australian museums and other institutions was very sparse, and in most instances also very old. During the period of Scott's studies of Tasmanian galaxiids (1930's onwards), a small but valuable collection of fishes was built up at the Queen Victoria Museum in Launceston. A small collection was also established at the Division of Fisheries and Oceanography, Commonwealth Scientific and Industrial Research Organisation, Cronulla. Before his major investigation of the fauna, Frankenberg collected widely in Australia and deposited a substantial collection of galaxiids in the National Museum of Victoria, Melbourne. Andrews (1976) also made a collection of galaxiids and the Tasmanian Museum, Hobart, has a useful collection of Tasmanian species. In 1969, D. E. Rosen and G. J. Nelson, of the American Museum of Natural History, New York, in the company of W. H. Butler, of Perth, Western Australia, collected fishes in a broad area of Western Australia, including a substantial collection of galaxiids. These collections are housed in the American Museum of Natural History, New York. Increased collecting activity by ichthyologists at the Western Australian Museum has added substantially to the collection of galaxiid fishes in that museum, and reconnaissance survey work by biologists at the Arthur Rylah Institute for Environmental Research, Division of Fisheries and Wildlife, Ministry of Conservation, Victoria, has produced a small but valuable collection of galaxiids. A similar, small collection is being assembled by the Tasmanian Inland Fisheries Commission, Hobart. Material collected by biologists of the New South Wales State Fisheries over the past 20 years, including some galaxiids, has been deposited in the Australian Museum, Sydney, and more recently, a survey of New South Wales freshwater fishes, conducted jointly by the Australian Museum and New South Wales State Fisheries under the financial support of the Australian Biological Resources Study, has substantially added to the collection of galaxiid and other fishes in the Australian Museum. Small collections are also housed in the Queensland Museum, Brisbane, the South Australian Museum, Adelaide, and in the zoology departments of some universities. A small collection is held by the Fisheries Research Division of the Ministry of Agriculture and Fisheries, Christchurch.

Material from all these collections was examined during preparation of this revision, as well as some very old type material housed in the museums of Europe. For most species large series of specimens were examined from a wide range of geographical localities. Samples from which morphometric and meristic data were taken are listed in Appendix 1. The material examined with distributional data is listed in a typescript available from the authors, and a copy has been deposited in the Fish Department, Australian Museum, Sydney.

Museum abbreviations: In listings of type and other material, institutions at which types are held are indicated by the following abbreviations:—
AIAC — Australian Institute of Anatomy, Canberra, A.C.T., Australia.
AMNH — American Museum of Natural History, New York, New York, U.S.A.
AMS — Australian Museum, Sydney, New South Wales, Australia.
BMNH — British Museum (Natural History), London, England.
FRD — Fisheries Research Division, Ministry of Agriculture and Fisheries, Christchurch, New Zealand.
FWDM — Fisheries and Wildlife Division, Ministry of Conservation, Heidelberg, Victoria, Australia.
MHNH — Museum National d'Histoire Naturelle, Paris, France.
MMS — Macleay Museum, University of Sydney, Sydney, New South Wales, Australia.
MNUB — Zoologisches Museum, Humboldt Universität, Berlin, Germany.
NMVM — National Museum of Victoria, Melbourne, Victoria, Australia.

NSWSF — New South Wales State Fisheries, Sydney, New South Wales, Australia.
QM — Queensland Museum, Brisbane, Queensland, Australia.
QVML — Queen Victoria Museum, Launceston, Tasmania, Australia.
RMNH — Rijksmuseum van Natuurlijke Historie, Leiden, Holland.
SAM — South Australian Museum, Adelaide, South Australia, Australia.
SMNS — Staatl Museum für Naturkunde, Stuttgart, Germany.
TIFC — Inland Fisheries Commission, Hobart, Tasmania, Australia.
TMH — Tasmanian Museum, Hobart, Tasmania, Australia.
WAM — Western Australian Museum, Perth, Western Australia, Australia.

Measurements and counts: Methods of measurement used were largely those described by Hubbs and Lagler (1958). Measurements were made with needlepoint dividers and determined to the nearest 0.25 mm, except when the limits of the structure being measured were difficult to determine, in which case measurements were to 0.5 mm. Measurements were taken as follows: total length — either length to caudal fork (L.C.F.), or if the caudal fin is rounded, to the posterior extremity of the fin (T.L.); standard length (S.L.); body depth at vent (B.D.V.) — used instead of greatest body depth because the latter is greatly affected by sexual maturity and distension of the stomach after feeding; depth of caudal peduncle (D.C.P.); length of caudal peduncle (L.C.P.) — measured from rear of anal fin base; predorsal length (PreD.); preanal length (PreA.); length of bases of dorsal and anal fins (L.D.B. & L.A.B.); greatest length of dorsal and anal fins (M.L.D. & M.L.A.); pectoral fin length (Pec.); pelvic fin length (Pel.); prepelvic length (PrePel.); pectoral-pelvic length (Pec.Pel.); pelvic-anal length (Pel.An.); head length (H.L.); head width (H.W.); head depth (H.D.) — taken vertically at the isthmus; snout length (Sn.L.); postorbital head length (P.O.H.L.); interorbital width (I.O.W.) — fleshy interorbital; diameter of eye (D.E.) — horizontal fleshy eye diameter; length of upper jaw (L.U.J.); length of lower jaw (L.L.J.); width of gape (W.G.).

The following structures were counted: fin rays in dorsal, caudal, anal, pectoral and pelvic fins; vertebrae; gill rakers; pyloric caeca. Counting fin rays in galaxiid fishes presents a minor problem since a variety of types of soft rays occurs. As in all salmoniform fishes, procurrent rays are present at the anterior ends of the dorsal, caudal and anal fins. Hubbs and Lagler (1958) recommended the inclusion of these procurrent rays in counts of the dorsal and anal fins in salmoniforms. This procedure was followed by Frankenberg, in his collection of data contributing to this revision. Many of his fin ray counts were taken from radiographs, and when these were not used, the counts were made by compressing the fins between microscope slides and examining them under a stereomiscroscope. For large and heavily pigmented specimens it was often necessary to expose the anterior rays of the median fins by dissection.

McDowall (1970a, 1972) has consistently used an alternative count. Because of the thick, fleshy nature of the fin bases in many galaxiids and because the anteriormost procurrent rays are in many instances extremely small, they are very difficult to count with any certainty. Alizarin stained preparations showed that there are from one to five such procurrent rays varying in size from a tiny, little-ossified splint to a strongly ossified but unbranched and unsegmented ray. Accordingly McDowall (1970a) adopted the technique of counting *only* and *all* segmented rays in the dorsal and anal fins, whether they branched or not. This procedure, which enables accurate and standardized counts, is more or less equivalent to a principal ray count (a count comprising all rays that reach the distal margin of the fin, and usually including one unbranched, segmented ray and all branched rays that follow). However, in the system adopted by McDowall (1970a) sometimes one or occasionally more unbranched, segmented rays are counted that do not reach the distal margin of the fin, (as they should to be counted in a principal ray count). This counting procedure establishes a definite and relatively easily determined starting point for counts on those species in which there is little or no branching of the fin rays. To enable comparison with results obtained by Frankenberg, and to also allow comparison with data obtained by McDowall in previous studies, counts of the dorsal and anal fin taken by McDowall in this study include both a total ray count, as used by Frankenberg, and a count of all segmented rays. Both sets of counts are presented in the tables of meristic data. The caudal fin ray count used was a standard principal ray count, i.e. a count of all branched rays plus the unbranched ray immediately above and below the branched rays. In paired fins all rays, except the very tiny, splint-like ray occasionally present, were counted, on one side only.

Vertebral counts were taken, usually, from radiographs, although sometimes from alizarin preparations; counts exclude hypural centra; i.e. the centrum carrying the parhypural, which forms the last haemal arch, was not included in the count. Gill rakers were counted on the first arch.

The disposition of laterosensory pores on the head, the number and size of the pyloric caeca, the occurrence of teeth on the tongue and mesopterygoids, and the presence or absence of enlarged canine teeth in the jaws were also determined.

All counts, whether of fresh material, alizarin preparations or radiographs, were made with a dissecting microscope.

Alizarin specimens were prepared using either the potassium hydroxide maceration technique of Hollister (1934) or the pancreatic enzyme digestion technique of Taylor (1967). In some instances cartilage was stained with toluidine blue (Burdi, 1965).

## SYSTEMATICS

Family Galaxiidae: The family Galaxiidae was formed by Müller (1844) to contain the genus *Galaxias* Cuvier (1817). The following family diagnosis is modified from McDowall (1970a):

DIAGNOSIS: Medium-sized to small fishes (30-600 mm), with 0-6 rudimentary to well-developed pyloric caeca, usually two. Both gonads well developed, although the left may be larger than the right, ovaries gymnoarian. Urinogenital aperture on a papilla set in a post-anal depression. Sexes usually similar, male nuptial tubercles not present. All species but one are believed to breed in fresh water, the exception in tidal river estuaries; some species confined to fresh water, either lacustrine or fluviatile, others diadromous with marine juveniles. Land-locked populations of diadromous species widespread.

Scales lacking, lateral line well developed, an accessory lateral line present dorso-laterally in some species. Laterosensory pores present on head.

Pelvic fins abdominal, 4-8 rays, usually 7, or occasionally fins absent. Caudal fin emarginate to rounded, less often forked, usually 16 principal rays (14 branched), procurrent rays usually well developed along caudal peduncle and also anterior to dorsal and anal fins; dorsal and anal fins originate well back on trunk, usually about level with vent (above pelvic fins only in *Paragalaxias*). Vertebrae 37-66; branchiostegals 5-9.

Maxilla partly included in gape but toothless; teeth on premaxilla and dentary uniserial, mesopterygoidal, basihyal, and pharyngeal teeth developed (reduced or absent in *Neochanna*); no supramaxilla; no vomerine teeth.

Parietals large, uniting broadly in a median suture, supraoccipital not in contact with frontals, excluded from foramen magnum. Posterior myodome open. Orbitosphenoid, basisphenoid, and proethmoids absent; supraethmoid and ventral ethmoid usually present. Posttemporal simple; no mesocoracoid. Epipleural and epineural ribs usually present; neural and haemal arches usually autogenous, anterior uroneural not fused to terminal vertebra; none of terminal vertebrae upturned, usually a single hypural vertebra, occasionally two. Caudal neural and haemal spines usually much compressed (not in *Galaxiella* and occasional *Galaxias* spp.).

**General and diagnostic characters.** Fishes of the family Galaxiidae present a varied but distinctive facies. The first observers (Forster, 1778; Bloch and Schneider, 1801) saw a resemblance to the Northern Hemisphere pikes (family Esocidae), probably because of the extremely posterior position of the dorsal and anal fins, and the long-jawed appearance of the single species with which they were acquainted (*Galaxias argenteus* (Gmelin) from New Zealand). However, these similarities are largely superficial; galaxiid fishes are scaleless, with thick, highly mucigerous, rather leathery skins. The head is usually moderately large, with prominent jaws, the upper and lower varying in proportional development so that the lower may protrude, recede, or be equal to the upper in length. Lateral line pores on the head are well developed, their disposition fairly constant, and related to the supraorbital, infraorbital, mandibular, and hyomandibular branches of the lateral-line system of the head (see Lagler et al., 1962). Minor interspecific variation occurs in the relative positions of these pores. The lowermost in the preopercular series of four pores may be displaced anteriorly. The pair of pores beneath the eye, one in the infraorbital series, the other in the mandibular series, also vary in relative positions, the infraorbital pore sometimes anterior and sometimes posterior to the mandibular pore. The pore usually postero-medial to the eye sometimes migrates laterally to the margin of the orbit, and in some species tends to migrate forwards to be medial to the eye. Pore numbers are consistent in all Australian *Galaxias* species except *G. parvus* and *G. fontanus* (Fig. 47).

Variation is greater in *Paragalaxias* and *Galaxiella,* with pores lost and pore positions more variable. In particular the mandibular pores have been lost in *Galaxiella* and in two species of *Paragalaxias*. Various modifications of the generalized galaxiid pattern are shown for the species of these genera in Fig. 47. The very large pores in *P. dissimilis* are notable, as is the confluence of the posterior nostril with one of the supraporbital pore series in three species of *Paragalaxias*.

The lateral line is well developed on the trunk from the upper edge of the opercular aperture to the middle of the tail base. In some species groups there is a dorsal accessory lateral line along the dorso-lateral trunk, evident as a more or less distinct linear series of small, widely-separated papillae from the occiput to about the dorsal fin.

The nostrils are well developed, the anterior one set in a small depression and tubular. In some species the anterior nostril is especially well developed, and may project forwards beyond the upper lip. The posterior nostril is a simple aperture.

The form of the mouth varies, the profile of the jaws from the ventral aspect varying from deep and narrow, U-shaped, to broad and shallow with the depth much less than the breadth.

The dorsal and anal fins are posterior; in most species the dorsal originates about level with the vent although it may originate above the pelvic fins (*Paragalaxias*), or somewhat behind the vent (*Brachygalaxias* and *Galaxiella*). When depressed the dorsal and anal fins may overlie the base of the caudal fin. These fins are variable in shape and size, are usually short-based, sometimes high and rounded, but in other instances much lower, the hind rays short, and the fin not extending back far beyond the fin base, or rays subequal in length, the fin long and low. The caudal fin varies from well-forked to much-rounded. The pelvic fins are usually rounded in shape and expansive; they originate at or a little behind the mid-point of the standard length. The pectoral fins are more variable in length and position; they may be quite high laterally with the lamina of the fin vertical, or low lateroventrally with the fin lamina tending to be more horizontal. In many species all the fins are thick and fleshy, especially at the bases.

Teeth are present on the premaxilla, dentary, basihyal and mesopterygoid, the pharyngobranchial of the third, the epibranchial of the fourth and the ceratobranchial of the fifth branchial arches. The basibranchial plate is toothless. Teeth on all but the basihyal and pharyngeal bones are uniserial; sometimes there is a tendency for teeth to be displaced laterally from the primary row which then appears partly biserial. Mesopterygoidal teeth are reduced or absent in the neochannoid species. The teeth are usually conical but in *Neochanna apoda* Günther (New Zealand) the jaw teeth are peculiarly flattened and incisor-like. In many species the jaw teeth are enlarged laterally as opposing groups of canines; one species has slightly enlarged, fang-like teeth at the mandibular symphysis. Associated with the toothed bones are unattached or decumbent teeth, which usually lie freely in the tissue covering the bones.

The structure of the ovaries in the family Galaxiidae was described as gymnoarian by Hoar (1957). Kendall (1922) examined the "oviducts" of some salmonoids and concluded that they are shallow, open troughs and not entirely lacking, and that they are not radically different from those of other primitive fishes. However, the reduced condition of the oviducts, as in the Salmonidae, persists throughout the salmoniform fishes. The condition is sufficiently different for Hoar to distinguish them from other ovarian types. Breder and Rosen (1966:614) followed Hoar, stating that in the Galaxiidae and other salmoniforms, the "ova pass into the peritoneal cavity and thence through the pores to the exterior". Henderson (1967) concluded that the eggs of salmonids are discharged into the abdominal cavity, and that proper oviducts are lacking.

Galaxiid fishes exhibit considerable plasticity in form. Most characters were found to vary from species to species and even characters which vary little, like pelvic and caudal fin ray counts, or disposition of cephalic laterosensory pores, were found to differ from the norm in several phylogenetic lineages. Stokell (1945) considered vertebral number to be the most important taxonomic character for the New Zealand galaxiid fauna. This has proved to be a useful character, but it is important to bear in mind the effect of temperature during development on vertebral number; wide variation in vertebral number has been documented in some galaxiids, e.g. *G. maculatus* 52-66 (McDowall, 1972).

Apart from vertebral number, important meristic characters include number of caudal, anal, pelvic and to a lesser extent dorsal and pectoral fin rays. The number of gill rakers exhibits interspecific variation. The most important morphometric characters were the following: length and depth of caudal peduncle, relative positions of the dorsal and anal fins, and their basal and maximum lengths, lengths of the pectoral and pelvic fins, length of the pelvic-anal interval, head length, eye diameter, lengths of upper and lower jaws, width of gape. The degree of development of canine and mesopterygoidal teeth, pyloric caeca and gill rakers exhibits inter-specific variation.

In some species groups and many species, colour pattern is diagnostically important, in spite of individual variation. In other species groups specific distinctness is clearly indicated by fundamental differences in the life history pattern, some species being diadromous with a distinctive marine juvenile stage, similar and related species being entirely freshwater without a distinctive juvenile form.

Most of the taxonomic characters used are conventional in ichthyology, but the morphological plasticity of the Galaxiidae results in a considerable diversity in such characters. Some are stable and unimportant throughout much of the family but show significant variation in certain species or species groups; other characters vary widely throughout the family.

**Relationships of galaxiid fishes.** The relationships of the family Galaxiidae remained obscure for many years. Early authors pointed to similarities between galaxiids and the esocoid fishes (families Esocidae and Umbridae), and at times the family has been assigned, with these families to the so-called Haplomi or Esociformes. Inasmuch as the esocoids were formerly well separated from the salmoniform fishes in postulated fish phylogenies, this was an important matter. However, beginning with Berg (1940), there has been a growing concensus that esocoids and salmonoids are closely related, and both Gosline (1960) and Greenwood et al. (1966) followed Berg in placing the two groups as coordinate suborders with close affinities. Close salmonoid affinities for the Galaxiidae were indicated by Weitzman's (1967) study, and this view was further strengthened by a study of the osteology of the Galaxiidae and the other southern hemisphere salmoniform fishes found in fresh waters (Aplochitonidae, Retropinnidae, Prototroctidae), by McDowall (1969). McDowall suggested that these four families form two distinct groups — Galaxiidae-Aplochitonidae and Retropinnidae-Prototroctidae, the four forming a suborder Galaxioidei which was thought to be derived from an osmerid or salmonid-like ancestry. Patterson (1970), however, suggested that the Galaxiidae-Aplochitonidae pair has a derivation in primitive salmoniforms distinct from the origin in the salmoniforms of the Retropinnidae-Prototroctidae. Nelson (1972) from an examination of the occurrence and disposition of laterosensory pores and papillary rows on the head concluded to the contrary, that the four families are closely related and included all four families in the single family Galaxiidae, with two subfamilies Galaxiinae and Retropinninae. Then Rosen (1974), primarily on the basis of osteological evidence, agreed with Patterson (1970); Rosen suggested that the galaxiid and aplochitonid fishes have close affinities with the Salmonidae and the retropinnid and prototroctid fishes with the Osmeridae. Rosen recognised only the families Galaxiidae (including Aplochitonidae) and Retropinnidae (including Prototroctidae).

Although Rosen included *Aplochiton* and *Lovettia* in the Galaxiidae, these two genera stand apart from galaxiids (*sensu stricto*), and they have been excluded from the family in this account. Whatever the familial arrangement of these groups, the salmoniform relationships of the galaxiid fishes are generally agreed upon.

**The genera of galaxiid fishes.** Some general comment on the approach to generic classification of galaxiid fishes is appropriate here as a prelude to discussion of the actual classification. Early workers were conservative in their use of new generic names, and by 1900 only three valid names had been proposed, of which two were in general use (*Galaxias* Cuvier and *Neochanna* Günther). *Brachygalaxias* Eigenmann followed in 1928. In the 1930's, Whitley (1935) proposed three new generic names, one of these mentioned in the text, but undiagnosed, the other two simply listed in the caption to a figure as "gen. nov." Scott (1935, 1936), on the other hand, first described *Paragalaxias* and then followed with his complex classification based on broad assemblages of characters of diverse types, but without any apparent analysis of the significance of these characters to phylogenetic relationships. Scott (1966) later reasserted the validity of his generic arrangement, somewhat modified, possibly, in part, in response to Stokell's (1945) general rejection of it. Use of even such normally stable characters as disposition of laterosensory pores on the head, is fraught with problems. For example, the loss of the submandibular pores occurs in the South African *G. zebratus,* in two of four Tasmanian species of *Paragalaxias* and in the three Australian species of *Galaxiella*. Since two of the *Paragalaxias* species retain these pores, their occurrence presumably being a primitive character and their loss derived, either all those species lacking the pores are derived through the *Paragalaxias* which retain the pores and which are therefore likely to be more primitive than other *Paragalaxias,* or the loss of the pores has occurred in several, probably three distinct galaxiid lineages. The former alternative seems highly unlikely, being quite unsupported by any other morphological evidence, and suggests that loss of the submandibular pores has occurred convergently at least two and possibly three times.

Study of the broad spectrum of galaxiid fishes suggests that the diadromous species are more generalised and primitive, and that there is a tendency for freshwater limited species to be more derived and specialised. This is indicated by the fact that all of the proposed galaxiid genera, apart from the type genus *Galaxias,* and with the exception of *Austrocobitis* Ogilby, refer to entirely freshwater dwelling species. The association between restrictions to fresh water and specialisation could be taken to indicate that common morphological peculiarities shared by freshwater limited species may be related to independent development of adaptations to specialised freshwater habitats and habits.

Reduction in the number of pelvic fin rays has occurred in widely divergent phylogenetic lineages. The number of rays is stable at seven in most species, but in *Brachygalaxias bullocki* (Eigenmann) (Chile), *G. zebratus* (Castelnau) (South Africa), *Neochanna burrowsius* (Phillipps), *G. divergens* Stokell, *G. gracilis* McDowall (New Zealand), *Galaxiella* species, *Paragalaxias* species, *G. cleaveri* Scott (Australia), there is reduction from seven to six or fewer. The classification adopted here is intended to reflect phylogenetic relationships, and generic distinctions are based as far as can be determined on characters that are not obviously plastic or prone to rapid modification. We have sought to apply this approach to the generic classification of the Australian Galaxiidae.

The first fish that can certainly be associated with the family Galaxiidae came from Dusky Sound, New Zealand, and was referred to the genus *Esox* (Forster, 1778; Gmelin, 1789; Bloch and Schneider, 1801). The genus *Galaxias* was established by Cuvier (1817) without the nomination or inclusion of a valid species of *Galaxias* in the genus. For this reason the type species is determined by subsequent usage and *Galaxias fasciatus* Gray (1842) is the type species by subsequent monotypy (McDowall, 1967a). *Galaxias* Cuvier (1817) predates *Galaxias* Beck (1837) — Mollusca.

Jenyns (1842) described several species in the new genus *Mesites,* apparently in ignorance of the previously described genus *Galaxias,* the name *Mesites* being further invalidated by preoccupation for a genus of beetles (Schoenherr, 1838). *Mesites* was also used for a genus of birds by Saint-Hilaire (1838).

Ogilby (1899) regarded Jenyns' species (*G. maculatus, G. attenuatus* and *G. alpinus*) as sufficiently distinct to warrant a separate genus, and as *Mesites* was preoccupied he proposed the name *Austrocobitis.* Günther (1866) after describing the 12 then known species in the genus *Galaxias* subsequently described a new species lacking pelvic fins in the new genus *Neochanna* Günther, (1867).

Regan (1905) in his general revision of the family Galaxiidae dealt with 26 species, but did not recognise *Austrocobitis.* Eigenmann (1928), in a systematic work on freshwater fishes in Chile, established the genus *Brachygalaxias* for *Galaxias bullocki* Regan (1908). *G. pusillus* Mack (1936) was subsequently included in *Brachygalaxias* by Scott (1942). The genus *Paragalaxias* was proposed by Scott (1935) for a Tasmanian species. In 1935 Whitley proposed three new genera — *Nesogalaxias* for *Galaxias neocaledonicus* Weber and de Beaufort (1913) — New Caledonia; *Lyragalaxias* for *Galaxias oconnori* Ogilby (1912) — Queensland; and *Querigalaxias* for *G. dissimilis* Regan (1905) — "New South Wales". None of these three genera was described or diagnosed by Whitley. Although *Nesogalaxias* was sustained and diagnosed by McDowall (1968a), neither of the other genera has been used or diagnosed by serious students of galaxiid fishes; *Querigalaxias* is a junior objective synonym of *Paragalaxias* Scott.

Scott (1936), in a revision of Tasmanian galaxiids, proposed a complex infrafamilial classification of the Galaxiidae, including a subfamily Paragalaxiinae for the genus *Paragalaxias* and a subfamily Galaxiinae for the remainder of the family. The genus *Galaxias* was subdivided into two subgenera — *Galaxias* and *Agalaxis* — (the latter to contain the single South African galaxiid *G. zebratus*); the genus *Neochanna* was sustained by Scott, and a new genus *Saxilaga* proposed, with two subgenera — *Saxilaga* and *Lixagasa*. Subsequently in a revision of New Zealand galaxiid fishes, Stokell (1945) excluded *Paragalaxias* from the family Galaxiidae and listed *Mesites, Austrocobitis, Brachygalaxias, Querigalaxias, Lyragalaxias, Nesogalaxias, Saxilaga* and *Agalaxis* as "Not Recognised". Stokell (1950) subsequently readmitted *Paragalaxias* to the Galaxiidae and later (1954) recognised *Brachygalaxias* for both South American and Australian species. Whitley (1965a, b, 1957, 1960) consistently used *Brachygalaxias* for Australian species and this usage has been adopted by Scott (1966, 1971a), Frankenberg (1966a, b, 1968), Lake (1971), and others.

Scott's (1936) complex infrafamilial classification was never adopted by other workers, and was partly abandoned by Scott himself (Scott, 1966). McDowall (1973b) examined the South African galaxiid and concluded that there are no grounds for retention of the genus *Agalaxis* for this species. Subsequently McDowall (1973c) examined the limits of the genus *Brachygalaxias* in relation to the type species *B. bullocki* from Chile and the Australian species included by some in this genus. He concluded that although there are certain similarities between *Brachygalaxias* and the Australian species, there is little evidence to indicate that the similarities are a result of any close phylogenetic relationship. *Brachygalaxias* was therefore limited to the Chilean species.

Although the inclusion of Australian species in *Brachygalaxias* is regarded as inappropriate by McDowall (1973c), the three Australian species which would, under Scott's (1942, 1966) criteria, be included in *Brachygalaxias* nevertheless form a close-knit and compact species group that very obviously has a close common ancestry that relates them to each other more closely than to other galaxiids. They certainly stand apart from the general array of galaxiid fishes at about the same level of distinction as do the three New Zealand species of *Neochanna,* the single New Caledonian species of *Nesogalaxias,* or the four Tasmanian *Paragalaxias,* and for this reason the establishment of the distinct genus seemed justifiable. No name was available for such a genus, and the name *Galaxiella* was proposed, a diminutive of *Galaxias* (McDowall, 1978a).

The genus *Saxilaga* Scott (1936) was diagnosed by its five or six pelvic fin rays, dorsal and anal fin rays simple or a mixture of simple and branched, and mesopterygoid toothless. Andrews (1976) has shown that all these characters vary within populations to such an extent that some individuals of the species that Scott (1936) places in *Saxilaga* belong in *Galaxias* (i.e. have seven pelvic fin rays, dorsal and anal rays branched, mesopterygoids toothed), while others belong in *Saxilaga*. Thus the distinction between *Saxilaga* and *Galaxias* breaks down at the population level, and *Saxilaga* cannot be retained.

As a result of this and previous studies on galaxiid fishes, the following genera are recognised:

*Galaxias* Cuvier — Australia, New Zealand, South America, South Africa (includes *Agalaxis* Scott, *Saxilaga* Scott, *Austrocobitis* Ogilby, and *Mesites* Jenyns.
*Neochanna* Günther — New Zealand.
*Paragalaxias* Scott — Tasmania.

*Brachygalaxias* Eigenmann — Chile.
*Nesogalaxias* Whitley — New Caledonia.
*Galaxiella* McDowall — Australia.

## KEY TO AUSTRALIAN GENERA OF GALAXIIDAE

1. Dorsal fin origin forward, above pelvic fin bases .......................*Paragalaxias* p.569

   Dorsal fin origin, posterior, distinctly behind pelvic fin bases, more or less above vent ..........................................................................................2

2. Dorsal fin origin distinctly behind anal origin; procurrent caudal fin rays reduced to 3-4; no laterosensory pores beneath lower jaw; less than 16 principal caudal rays, usually 13-14 ..........................................*Galaxiella* p.552

   Dorsal fin origin usually above or a little in front of anal origin; procurrent caudal fin rays more than 3-4; laterosensory pores present beneath lower jaw; usually 16 principal caudal rays ..........................................*Galaxias* p.455

## Genus **Galaxias** Cuvier

*Galaxias* Cuvier, 1817: 183 (type species *Galaxias fasciatus* Gray, 1842, by subsequent monotypy).

*Mesites* Jenyns, 1842: 118 (type species *Mesites attenuatus* Jenyns, 1842, by subsequent designation, Jordan, 1919: 212, preoccupied by *Mesites* Schoenherr, 1838, Coleoptera).

*Austrocobitis* Ogilby, 1899: 158 (type species *Mesites attenuatus* Jenyns, 1842, by subsequent designation, Whitley, 1956a: 34).

*Saxilaga* Scott, 1936: 106 (type species *Galaxias cleaveri* Scott, 1934, by original designation).

DIAGNOSIS: Trunk cylindrical to a little compressed, naked; dorsal fin origin very posterior, about above vent. Pelvic fins present, six to eight rays, usually seven; pectoral fin positioned laterally to low lateroventrally. Caudal fin with 16 principal rays, occasionally fewer. Jaw teeth conical, uniserial, with or without enlarged lateral canines; mesopterygoidal teeth well developed to rudimentary, uniserial; lingual teeth biserial. Median supraethmoid and ventral ethmoid present; postcleithrum present or absent; epipleural and epineural ribs present.

## KEY TO AUSTRALIAN SPECIES OF *GALAXIAS*

1. Caudal fin distinctly rounded..........................................................................2.
   Caudal fin emarginate to forked.....................................................................3.

2. Vertebrae 44-49; no pyloric caeca; 3 preopercular pores (Lake Pedder area, Tasmania) ..........................................................................*G. parvus* p.523
   Vertebrae 56-60; 2 long pyloric caeca; 4 preopercular pores (Tasmania, low elevations in north, west and south-east) ...............................*G. cleaveri* p.519

3. Usually 5-6 pores in series from below eye to anterior nostril (Swan River, eastern Tasmania ............................................................*G. fontanus* p.498
   Four pores in series from below eye to anterior nostril ...................................4

4. Gill rakers short and stout; anal fin origin usually below middle of dorsal, or further back..........................................................................................5
   Gill rakers long and slender; anal fin origin below dorsal origin or as far back as mid-dorsal ..........................................................................................7

5. 2 pyloric caeca of moderate length (Clarence Lagoon, Tasmania). G. johnstoni p.489
   0-1 pyloric caeca, occasionally 2 ............................................................................6

6. Head short and bluntly rounded; usually 14-16 pectoral fin rays (widespread in southeastern Australia) ..........................................................*G. olidus* p.469
   Head longer, flattened above and tapering to a slender snout; usually 12-13 pectoral fin rays. (Lake Pedder, Tasmania) ........................*G. pedderensis* p.493

7. Pyloric caeca long; lower jaw shorter than upper (coastal drainage from about Sydney to Adelaide, also Tasmania) ...................................*G. brevipinnis* p.456
   Pyloric caeca reduced to vestiges, or lacking, jaws about equal........................8

8. Caudal fin forked; pec./pec.pel. and pel./pel.an. ratios less than 50%; fish slender bodied.........................................................................................9
   Caudal fin truncate to emarginate; pec./pec.pel. and pel./pel.an. ratios more than 50%; chunky and deep bodied..........................................................11

9. Mouth small, reaching only to front of eyes (coastal drainages of New South Wales, Victoria, South Australia, Tasmania and southern coast of Western Australia) .........................................................*G.maculatus* p.526
   Mouth larger, reaching distinctly below eyes..............................................10

10. Small fangs at mandibular symphysis and lateral canines developed; distinct, bold, paired vertical bands along sides (southwestern Western Australia) .....................................*G. occidentalis* p.542
    No fangs or canine teeth; little pigmentation and no bands on sides. (Murray-Darling drainage) ..................................................*G. rostratus* p.549

11. Dorsal, anal and pelvic fins with grey-black margins.....................................12
    Dorsal, anal and pelvic fins without grey-black margins. (Arthurs Lake, Tasmania) ...............................................................*G. tanycephalus* p.516

12. Widely spaced, occellated, round spots along sides, distinct dark blotch, sometimes split into two, behind opercular opening and above pectoral fin base; vertebrae 56-62, usually more than 59 (Victoria and Tasmania, also southern Western Australia) .............................................*G. truttaceus* p.501
    Closely spaced, vertical occellated bars along sides, these becoming fragmented into vertical series of ovoid blotches; no distinct dark blotch behind opercular opening; vertebrae 53-56. (Lakes Sorell and Crescent, Tasmania) ........................................................................*G. auratus* p.512

## **Galaxias brevipinnis** Günther

Fig. 1, 3

*Galaxias brevipinnis* Günther, 1866: 213 (syntypes: (3) BMNH 1853.2.14: 5-7, not seen; type locality; New Zealand); McDowall, 1970b: 18; 1971: 65; Lake, 1971: 20; Andrews, 1973: 104; Lynch, 1974: 11; Andrews, 1976: 312; Lynch, 1977: 14; McDowall, 1978c: 61; 1978d: 97; McDowall and Fulton, 1978b: 663; Fulton, 1978b: 3; Lake, 1978: 26; Backhouse and Vanner, 1978: 128.

*Galaxias coxii* Macleay, 1881: 45 (syntypes: (3) formerly MMS, now AMS I.16262-001,*

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* Macleay's types were originally held in the Macleay Museum at Sydney University, and were listed by Stanbury (1969) as "Approx. 14", no. F 87. The collection at the Macleay Museum was transferred to the Australian Museum, and the label in the jar states "14? specimens, 2 jars". But all the specimens are in one jar and there are 21 fish. Amongst these 21 fish are presumably the three syntypes mentioned by Macleay as being "seven inches long". All of the 21 specimens appear to belong to the same species, although this will always remain uncertain owing to the very poor condition of some of them. The source of the 18 fish additional to the three syntypes is unknown. Regan (1905), when redescribing *G. coxii* stated that "The specimens (4) received from the Australian Musuem without name and without locality evidently correspond to Macleay's *Galaxias coxii* from Mount Wilson . . . and may probably be regarded as the types of that species". This cannot be correct as Macleay nominated only three types which were in the Macleay Museum in Regan's time.

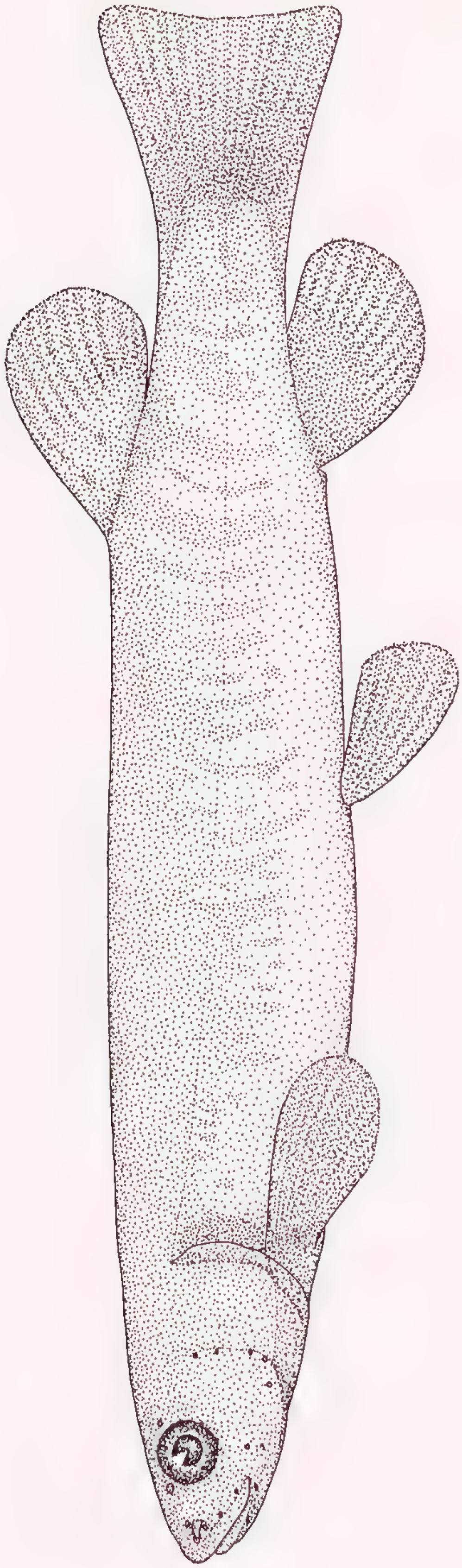

Fig. 1. *Galaxias brevipinnis* Günther; Gerringong Creek, Kangaroo Valley, N.S.W. 121 mm L.C.F.

seen; type locality: a small rivulet on or near the summit of Mount Wilson, Colo River, New South Wales); 1882: 232; Ogilby, 1886: 54; 1893: 176; 1896: 69; Waite, 1904: 16; Regan, 1905: 380; Stead, 1906: 50; 1908: 33; Zietz, 1908: 297; Gale, 1915: 16; Waite, 1921: 42; McCulloch, 1921: 28; 1922: 18; 1927: 18; 1929: 48; Mack, 1936: 99; Butcher, 1946: 9; Whitley, 1956a: 30; 1956b: 39; 1957a: 7; 1957b: 10 (*partim*); Munro, 1957b: 17; Littlejohn, 1962: 311; Whitley, 1964: 35; Williams, 1964: 14; Frankenberg, 1966a: 162; 1966b: 20; 1967: 22; McDowall, 1968c: 157; Stanbury, 1969: 205; Scott, 1971a: 8; Lake, 1971: 20; Green and McGarvie, 1971: 30; Dixon, 1972: 121; Frankenberg, 1974: 119; Tilzey, 1974: 12 *(partim?);* Timms, 1974: 277; Tilzey, 1976: 555.

*Galaxias weedoni* Johnston, 1883: 131 (holotype: unknown — Whitley 1929, designated a figure of *G. weedoni* as the type but this is not a type of any recognised sort; type locality: Mersey River, Tasmania); Seal et al., 1883: lvi; Macleay, 1885: 56; Ogilby, 1896: 70; Regan, 1905: 371; Lord, 1923: 63; Lord and Scott, 1934: 33; McCulloch, 1929: 47; Whitley, 1929: 46; Scott, 1934: 46; Whitley, 1956a: 34; 1956b: 39; 1957a: 7; Munro, 1957b: 16; Gentilli, 1961: 488; Whitley, 1964: 35; Lynch, 1965: 13; 1966: 13; Stokell, 1966: 76; Scott, 1968: 26; Lynch, 1969: 23; McDowall, 1970a: 371; Scott, 1971b: 120; 1974: 254; McLean, 1974: 13.

*Galaxias atkinsoni* Johnston, 1883: 121 (holotype: unknown; type locality: Pieman River, Tasmania); Seal et al., 1883: lvi; Macleay, 1885: 56; Ogilby, 1896: 69; Whitley, 1956a: 34; 1964: 35.

*Galaxias nigothoruk* Lucas, 1892: 27 (syntypes: (4) NMVM A.408-411, seen, BMNH 1891.9.24:44 not seen*; type locality: Lake Nigothoruk = Lake Tali Karng, Victoria); Ogilby, 1896: 70; Dendy, 1919: 326; Stokell, 1947: 671; Whitley, 1956a: 34; 1956b: 39; 1964: 35.

*Galaxias affinis* Regan, 1905: 380 (*partim;* syntypes:(3) BMNH 1893.6.15. 12-14, seen;(1) AMS I.7435, seen; specimens I.7434 (2), not types; type locality: Lake St. Clair, Tasmania); Lord, 1927: 12; McCulloch, 1929: 48; Scott, 1934: 39; Whitley, 1956a: 34; 1956b: 39; 1957a: 7; Munro, 1957b: 17; Whitley, 1964: 35; Stokell, 1966: 76; Scott 1968: 7; Frankenberg, 1968: 272; Fryer, 1969: 52; Lake, 1971: 20.

*Galaxias weddoni* — Lord, 1927: 12 (mis-spelling of *G. weedoni* Johnston).

*Galaxias (Galaxias) parkeri* Scott, 1936: 99 (holotype: BMNH 1937.4.3:1, seen: paratypes (11) BMNH 1937.4.3: 2-10, seen; (6) QVML 1971.5: 20-23, seen; (4) AMS IA.6414, seen; Scott indicated that he intended sending paratypes to the Museo Argentina Ciencias Naturales, Buenos Aires, the Australian Institute of Anatomy, Canberra, the Musuem of the Department of Biology, University of Tasmania, and the Tasmanian Museum, Hobart; these were apparently never sent; type locality: Great Lake, off Howell's Neck, Tasmania) 1941: 60; 1942: 541.

*Galaxias (Galaxias) affinis* — Scott, 1936: 91; 1938: 120.

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*Regan (1905:380), when synonymising *G. nigothoruk* and *G. coxii* stated that he had examined a specimen "(95 mm) one of the type(s?) of *G. nigothoruk*, Nigothoruk, Victoria", received from Professor A. Dendy. Dendy worked for a time in Victoria (with A. H. S. Lucas who described *G. nigothoruk),* before leaving for New Zealand. Whether the specimen he sent to Regan is, in fact, a type is unclear and Regan's comments on the status of *G. coxii* specimens he was sent suggest that he, in some instances, assumed that he was being sent type material. The status of the British Museum specimen of "*G. nigothoruk*" is indeterminate and is likely to remain so.

*Galaxias (Galaxias) weedoni* — Scott, 1936: 91; 1941: 60; 1942: 54.

*Galaxias parkeri* — Whitley, 1956a: 34; 1956b: 30; 1957a: 7; 1957b: 10; Munro, 1957b: 16; Gentilli, 1961: 488; Lynch, 1967: 20; Whitley, 1964: 35; Scott, 1968: 8; Frankenberg, 1974: 119; Green 1974: 3.

*Galaxias truttaceus truttaceus* — Scott, 1962: 68; (non *Galaxias truttaceus* Valenciennes).

*Galaxias truttaceous* — Scott, Glover and Southcott, 1974: 77; (non *Galaxias truttaceus* Valenciennes).

Additional synonyms from the New Zealand region:
*Galaxias campbelli* Sauvage, 1880: 229.
*Galaxias lynx* Hutton, 1896: 317.
*Galaxias robinsoni* Clarke, 1899: 89.
*Galaxias bollansi* Hutton, 1901: 198.
*Galaxias huttoni* Regan, 1905: 373.
*Galaxias castlae* Whitley and Phillipps, 1940: 229.
*Galaxias koaro* Phillipps, 1940: 35.
*Galaxias kaikorai* Whitley, 1956c: 34 (see McDowall, 1970a, 1976a).

TAXONOMY: *G. brevipinnis* is a relatively little known and infrequently collected species in continental Australia, although it is better known in Tasmania through the work of Scott (1936) and as a component of the Tasmanian whitebait fishery (Lynch, 1965, 1966, 1974).

Until 1970 (McDowall, 1970b) it was known as *G. weedoni* Johnston and *G. parkeri* Scott in Tasmania and as *G. coxii* Macleay in the mainland. The name *G. affinis* Regan (Tasmania) had not been assigned to any known species although Mack (1936) considered *G. affinis* to be doubtfully distinct from *G. coxii*. A tentative suggestion that *G. weedoni and G. parkeri* are synonyms of *G. brevipinnis* Günther (New Zealand — McDowall, 1970a) was supported by the study of additional material from Tasmania (McDowall, 1970b) and further supported by Andrews (1976) in a review of the Tasmanian galaxiid fauna. Andrews also assigned *G. coxii* (Australian mainland) and *G. affinis* to the synonymy of *G. brevipinnis*. However, Frankenberg (1974) retained the names *G. coxii* for diadromous populations and *G. parkeri* for lacustrine populations in Tasmania although he affirmed that these two species, with *G. brevipinnis,* form a closely related species group. The group is distinguished by the elongate, rather slender form; depressed head, distinct canines laterally in both jaws; moderate to large pectoral fins that are placed low on the body with the lamina directed ventrally; short dorsal and anal fins with the anal origin well behind the dorsal origin; caudal peduncle much longer than deep; two pyloric caeca; and, usually, a prominent blue-black patch above the pectoral fin base.

Extensive data on material from Australia do not reveal any significant differences in form or meristic characters between populations usually referred to as *G. coxii* in Australia and *G. brevipinnis* in New Zealand. Comparision of the Australian data with New Zealand figures (Table 1; Fig 2) shows that New Zealand counts of fin rays and vertebrae are a little higher than Australian ones, but overlap is broad, variation between Australian populations about as broad as differences between Australian and New Zealand ones, and the differences not more than could be expected from clinal variation along about 20½° of latitude (about 2,300 km).

Vertebral number in the Australian populations is lower than in New Zealand ones, but this difference is continuation of an observed northwards increase in vertebral counts in the New Zealand populations (McDowall 1970a) (Fig. 3).

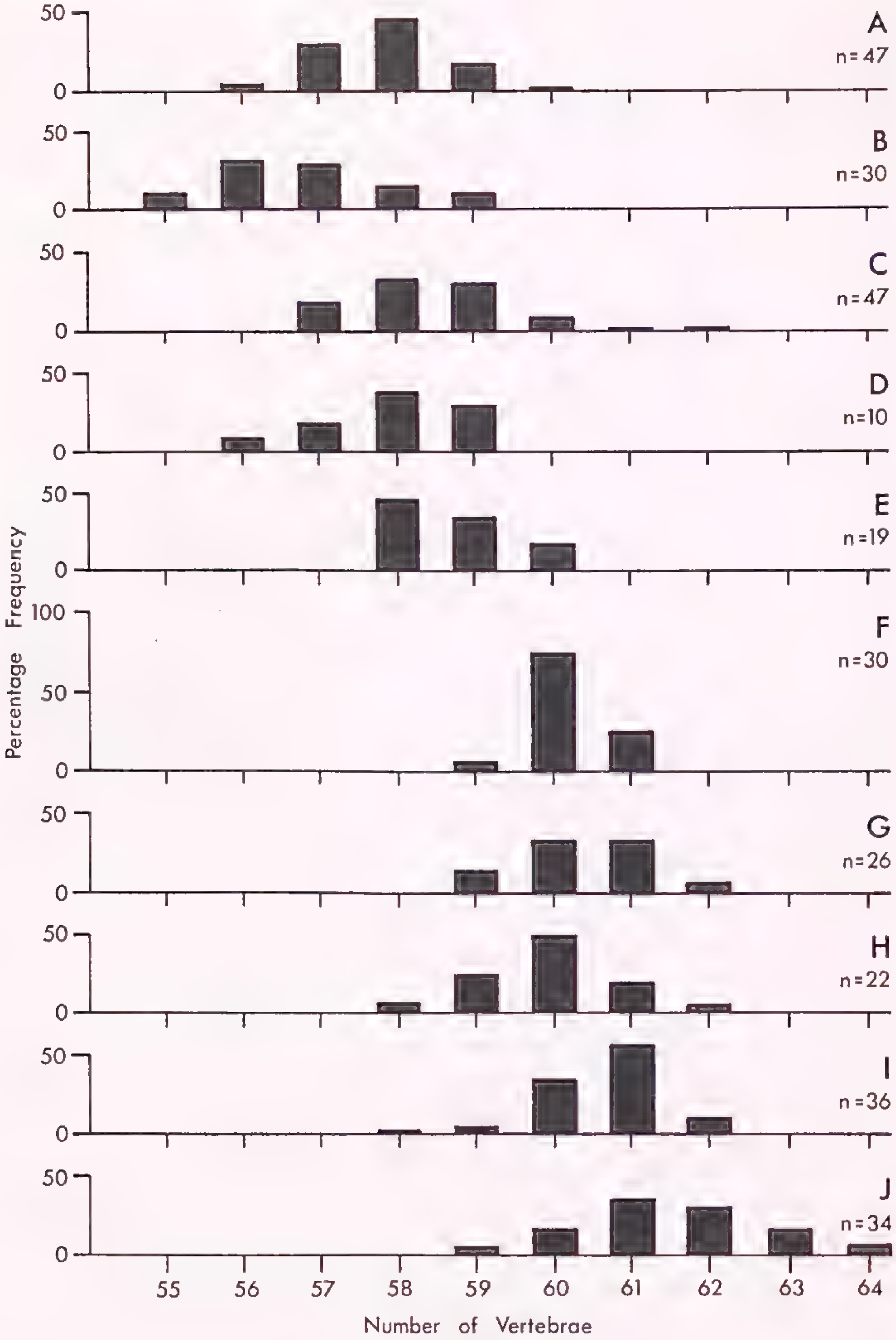

Fig. 2. Variation with latitude in the number of vertebrae in *Galaxias brevipinnis;* **a.** New South Wales; **b.** South Australia; **c.** Victoria; **d.** Flinders Island; **e.** Northern Tasmania; **f.** North Auckland, New Zealand; **g.** Wellington, New Zealand; **h.** Mid West Coast South Island, New Zealand; **i.** Haast, New Zealand; **j.** Auckland and Campbell Islands.

Body proportions in populations from the two areas are very similar, the most substantial differences being in the size of the pectoral fins and width of the interorbital. In most characters Australian and New Zealand forms are virtually inseparable. Although not evident in measurements, observations suggest that the jaws tend to be more equal in length in Australian populations, particularly those in the Blue Mountains.

Colouration of Australian populations is more variable. In most areas there is the prominent blue-black patch above the pectoral fin. Juveniles have distinctive chevron-shaped bands across the sides. In all populations these bands tend to become fragmented into irregular blotching or patching, but remain in some fish in all areas until adult size is reached. In New Zealand, colour development goes no further than this. In Tasmanian populations there is a tendency in some fish for the chevron bands to fragment into round spots rather than irregular blotching, and it appears that with the decrease in latitude, this tendency is accentuated, fish in populations from the north being more often spotted than blotched. However, colouration is immensely variable, a single population containing a very wide range of colour patterns (Fig. 2). It appears that in New Zealand, at the southern limits of the species' range, development of colour pattern is abbreviated and less variable than in more northern Australian populations.

There seems little justification for treating *G. brevipinnis* and *G. coxii* as distinct, and the view of Andrews (1976) is adopted here, with *G. brevipinnis* the senior synonym.

Regan's (1905) name *G. affinis* was treated as a junior synonym of *G. brevipinnis* by Andrews (1976:313), although he commented only that "results of the present study confirm . . . *G. coxii* and *G. affinis* are also synonyms of *G. brevipinnis*". Several characters in Regan's (1905) description clearly indicate the identity of *G. affinis* — distinct lateral canine teeth, small eyes (18.2-23.1% of head length), rather short dorsal and anal fins (total rays 10-12 and 12-14 respectively), anal origin below middle of dorsal fin, large pectoral and pelvic fins, long, slender caudal peduncle (D.C.P./L.C.P. 66.7-75.1%), and the "dark vertical bar above the base of the pectoral fin" (Regan, 1905:380). Examination of the syntype of *G. affinis* in the Australian Museum confirms its identity as *G. brevipinnis*.

In addition to the types from Lake St Clair, Regan (1905) also examined two smaller fish (73 and 78 mm long) from "Tasmania" which are also in the Australian Museum (No. I 7434). These are listed as syntypes by Andrews (1976) but they were not designated as types by Regan, and they are not *G. brevipinnis*. They do not have enlarged lateral canines, have small pectoral (Pec./Pec.Pel 36.2-40.7%) and pelvic (Pel./Pel.An 40.0-46.8%) fins, and have only a single pyloric caecum. They belong to the *G. olidus* species group (see p.469).

As these specimens were not designated as types by Regan (1905), there is no problem as to the specific identity of the types of *G. affinis* and designation of a lectotype is not necessary.

Study of populations over a wide area of New South Wales, Victoria, South Australia and Tasmania gave little evidence of meaningful patterns of variation except for an increase in the number of vertebrae relating to increasing latitude (Fig. 3). Northern populations have fewer vertebrae than southern ones. The population in Great Lake (Tasmania) has distinctly fewer vertebrae. Reduced vertebral counts have also been reported in New Zealand landlocked populations and this is presumably the explanation for low counts in Great Lake *G. brevipinnis;* this species becomes landlocked very easily, lake populations being abundant in New Zealand, some of them established in historic times (McDowall, 1970a). Body proportions did not appear to vary in any regular fashion, although limitations in the amount of material available for study, and the great age of some of it, hindered a full analysis of variation patterns.

DIAGNOSIS: Characterised by large, low-placed pectoral and pelvic fins, anal fin origin being distinctly behind dorsal origin, thick fleshy fins, presence of enlarged canine teeth in the jaws, and of a large, dark patch above and behind the pectoral fin base.

Differs from *G. olidus* and *G. pedderensis* in having the bold dark patch above the base of the pectoral fin, in having large canine teeth laterally in the jaws, larger paired fins and two long pyloric caeca; differs from *G. johnstoni* in these characters, except that both have two pyloric caeca; differs from *G. truttaceus* and *G. auratus* in having anal fin origin well behind dorsal origin, a long and relatively slender caudal peduncle, and two long pyloric caeca.

DESCRIPTION: A large, elongate and slender bodied species, the trunk rounded in section, the belly slightly deepened, especially approaching sexual maturity, but dorsal and ventral profiles about parallel; depressed anteriorly on head and compressed behind vent. Caudal peduncle moderately long and slender, longer than deep. Head moderately long, flattened and broader than deep, cheeks broadening below eyes. Snout flattened and somewhat rounded, broad. Mouth slightly oblique, large, extending back well below eyes, lower somewhat shorter than upper. Eyes small, deep in lateral head, interorbital convex but flattened dorsally. Jaws with prominent canines laterally; mesopterygoidal and lingual teeth well developed; gill rakers of moderate length, stout (Fig. 43); two long pyloric caeca (Fig. 45). Laterosensory pores on head as in Fig. 47.

Fins well developed, thick and fleshy at bases; dorsal and anal fins short-based but high and rounded, extending back well beyond bases; anal origin set well back from dorsal origin. Pectoral fins expansive inserted low latero-ventrally with lamina of fin directed ventrally. Pelvic-anal interval short, pelvic fins long and expansive, inserted at about mid-point of standard length. Caudal fin truncated to slightly emarginate, fin tips somewhat rounded, fin depth about equal to body depth, peduncle flanges moderately developed.

Variation: meristic: see Table 1
morphometric: see Table 2.

COLOUR: Colour in life is a dark greyish-brown, darker on the back and paling somewhat on the sides, the belly a dull silvery-olive. There is a distinct blue-black blotch behind the opercular opening and above the pectoral fin base. In sunlight there is prominent golden iridescence along the back and sides in some fish. Colour pattern is highly variable and changes with growth (Fig 3). Juveniles have variable distinct chevron-shaped bands across the sides. These may persist with growth, be replaced with irregular and variable blotching, or may disappear and be replaced with fine mottling without a bold pattern. Or the fish may pass through a transition from chevron bars to round spots arranged along the chevrons, to irregularly dispersed spots, most prominent towards the tail.

In preservative the fish fade to a dull blue-grey with grey-white markings, the belly a silver-grey. After long storage they become a dull brownish colour.

SIZE: In Australia *G. brevipinnis* reaches a known maximum size of about 214 mm total length and commonly attains 150-170 mm. In New Zealand it has been recorded up to 278 mm.

HABITAT: *G. brevipinnis* is found most often in clear-flowing, rocky or bouldery streams, often deeply shaded, and often in the fast flowing water. It seems sensitive to

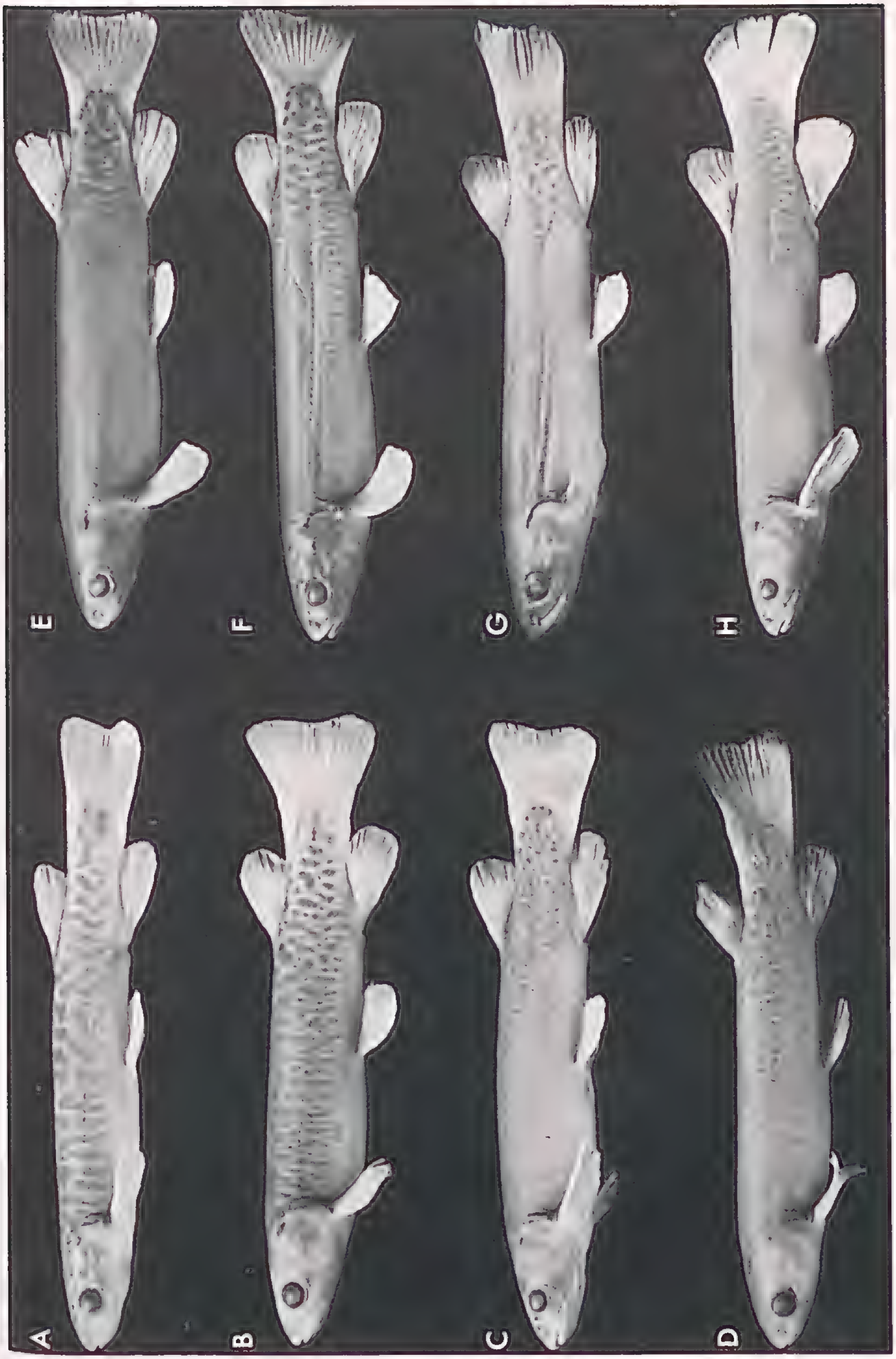

Fig. 3. Variation in colour pattern in *Galaxias brevipinnis* Gerringong Creek, Kangaroo Valley, N.S.W.: **a.** 86.5 mm L.C.F.; **b.** 102 mm L.C.F.; **c.** 115 mm L.C.F.; **d.** 122 mm L.C.F.; **e.** 123 mm L.C.F.; **f.** 124 mm L.C.F.; **g.** 135 mm L.C.F.; **h.** 133 mm L.C.F.

Table 1. Meristic variation in *Galaxias brevipinnis.*

| | | Ourimbah, N.S.W. | Blue Mountains, N.S.W. | Moss Vale, N.S.W. | South Australia | Buchan-Lang Lang, Vic. |
|---|---|---|---|---|---|---|
| Dorsal rays — segmented | 9 | | 2 | 9 | 6 | |
| | 10 | 7 | 8 | 15 | 6 | |
| | 11 | 2 | 3 | 3 | 3 | |
| | 12 | | | | | |
| total rays | 11 | | | | 1 | |
| | 12 | | 6 | 9 | 4 | 1 |
| | 13 | 4 | 5 | 31 | 7 | 6 |
| | 14 | 3 | 1 | 12 | 3 | 10 |
| | 15 | | | | | |
| | 16 | | | | | |
| Anal rays — segmented | 9 | | 1 | | | |
| | 10 | | 5 | 4 | 4 | |
| | 11 | 4 | 6 | 14 | 8 | |
| | 12 | 3 | 1 | 7 | 3 | |
| | 13 | | | 2 | | |
| total rays | 12 | | 2 | | | |
| | 13 | | 2 | 3 | 4 | 2 |
| | 14 | 3 | 4 | 13 | 6 | 5 |
| | 15 | 4 | 4 | 23 | 4 | 9 |
| | 16 | | 1 | 11 | | 1 |
| | 17 | | | 2 | | 1 |
| Pectoral rays | 12 | | 1 | | 1 | |
| | 13 | 1 | 6 | 4 | 5 | 4 |
| | 14 | 2 | 5 | 18 | 7 | 10 |
| | 15 | 4 | 1 | 3 | 2 | 2 |
| | 16 | | | | | 1 |
| | 17 | | | | | |
| Gill rakers | 11 | | | | | |
| | 12 | | 1 | 5 | | |
| | 13 | 6 | 6 | 12 | 3 | |
| | 14 | 2 | 5 | 9 | 10 | |
| | 15 | | 1 | | 2 | |
| | 16 | | | | | |
| | 17 | | | | | |
| Vertebrae | 52 | | | | | |
| | 53 | | | | | |
| | 54 | | | | | |
| | 55 | | | | 3 | |
| | 56 | | 2 | | 10 | |
| | 57 | 2 | 3 | 9 | 9 | 7 |
| | 58 | 5 | 6 | 11 | 5 | 7 |
| | 59 | | 4 | 4 | 3 | 5 |
| | 60 | | | 1 | | 1 |
| | 61 | | | | | 1 |
| | 62 | | | | | 1 |
| | 63 | | | | | |
| | 64 | | | | | |

| Otways, Vic. | Flinders Island | Cradle Valley, Tas. | Lake King William, Tas. | Pine Creek E. Tasmania | Lake Eucumbene, N.S.W. | Lake Tarli Karng, Vic. | Great Lake, Tas. | Lake Timk, Tas. | New Zealand |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | | | | | | 8 | 2 | 30 |
| 12 | 4 | | | | 1 | | 16 | 6 | 126 |
| 2 | 1 | | | | 1 | | 1 | 2 | 54 |
| | | | | | | | | | 7 |
| 1 | | | | | | | 2 | | |
| 5 | 7 | | 8 | | 1 | 1 | 12 | 4 | |
| 20 | 5 | 3 | 1 | 5 | | 1 | 8 | 5 | |
| 12 | 5 | 8 | | 10 | 1 | 2 | 3 | 1 | |
| 2 | | | | 2 | | | | | |
| 2 | | | | | | | | | 3 |
| 4 | 1 | | | | | | 9 | 1 | 21 |
| 8 | 4 | | | | 1 | | 14 | 3 | 113 |
| 1 | 2 | | | | 1 | | 2 | 6 | 61 |
| | | | | | | | | | 18 |
| 1 | 3 | | 1 | | | 1 | 12 | 1 | |
| 8 | 7 | | 4 | 1 | 1 | 2 | 11 | 4 | |
| 17 | 6 | 9 | 3 | 8 | | 1 | 2 | 4 | |
| 9 | 1 | 2 | 1 | 6 | 1 | | | 1 | |
| 5 | | | | 2 | | | | | |
| | | | 1 | | | | | | |
| 6 | 2 | | 1 | 1 | 1 | | 4 | | 4 |
| 27 | 4 | 5 | 3 | 2 | 1 | | 14 | | 50 |
| 7 | 1 | 6 | 2 | 12 | | | 6 | 3 | 113 |
| | | | 2 | 2 | | | 1 | 7 | 48 |
| | | | | | | | | | 2 |
| | | | | | | | | 1 | |
| 1 | | | | | | | | 3 | 6 |
| 2 | 2 | | | | | | | 1 | 73 |
| 12 | 2 | | | | | | | 5 | 57 |
| | 3 | | | | | | | | 22 |
| | | | | | | | | | 8 |
| | | | | | | | | | 1 |
| | | | | | | | | | 1 |
| | | | | | | | | | 2 |
| | | | | | | | 1 | | 9 |
| | | | | | | | 2 | | 16 |
| | 1 | | | | | 1 | 5 | | 30 |
| 2 | 2 | | 1 | 1 | | 2 | 7 | | 45 |
| 9 | 4 | 9 | 2 | 1 | | 1 | 6 | | 36 |
| 10 | 3 | 7 | 3 | 8 | 2 | | 4 | 2 | 53 |
| 4 | | 3 | 2 | 3 | | | | 8 | 77 |
| | | | 0 | | | | | 5 | 63 |
| | | | 1 | | | | | | 16 |
| | | | | | | | | | 5 |
| | | | | | | | | | 2 |

Table 2. Morphometric variation in *Galaxias brevipinnis*.
Figures are given as percentages of denominators in ratios.

| | | S.L./T.L. | B.D.V./S.L. | L.C.P./S.L. | D.C.P./L.C.P. | Pre D./S.L. | Pre D./Pre A | L.D.B./S.L. | M.L.D./L.D.B. | L.A.B./S.L. | M.L.A./L.A.B. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ourimbah, N.S.W. | Mean | 86.70 | 13.97 | 13.63 | 73.84 | 72.79 | 93.99 | 10.93 | 185.59 | 11.66 | 175.67 |
| | S.D. | 0.94 | 1.26 | 1.12 | 9.11 | 2.20 | 2.46 | 0.98 | 13.81 | 0.61 | 12.65 |
| Blue Mountains, N.S.W. | Mean | 87.48 | 14.54 | 11.78 | 84.71 | 74.76 | 94.95 | 9.65 | 195.32 | 11.18 | 179.94 |
| | S.D. | 1.22 | 1.11 | 0.91 | 8.44 | 1.27 | 2.41 | 0.83 | 8.36 | 0.96 | 12.59 |
| Moss Vale, N.S.W | Mean | 87.45 | 15.29 | 12.73 | 84.30 | 74.79 | 96.06 | 9.97 | 183.11 | 11.68 | 165.59 |
| | S.D. | 1.04 | 0.52 | 0.65 | 4.05 | 0.83 | 1.10 | 0.58 | 9.02 | 0.61 | 11.05 |
| South Australia | Mean | 87.18 | 12.72 | 13.06 | 72.11 | 74.05 | 93.71 | 9.79 | 187.79 | 10.53 | 179.12 |
| | S.D. | 1.04 | 0.82 | 0.77 | 6.83 | 1.41 | 1.81 | 1.13 | 12.99 | 0.88 | 10.23 |
| Otways, Vic. | Mean | 87.49 | 14.65 | 13.41 | 78.78 | 74.51 | 95.98 | 10.12 | 179.74 | 11.59 | 166.53 |
| | S.D. | 0.85 | 0.87 | 1.02 | 8.46 | 1.49 | 1.36 | 0.86 | 14.69 | 0.87 | 13.45 |
| Flinders Island | Mean | 87.00 | 12.79 | 13.06 | 73.19 | 73.21 | 94.00 | 9.44 | 196.31 | 11.34 | 175.97 |
| | S.D. | 0.73 | 0.77 | 0.75 | 5.74 | 1.52 | 1.74 | 0.46 | 15.55 | 0.67 | 9.18 |
| Great Lake, Tas. | Mean | 87.92 | 12.94 | 13.7 | 70.80 | 72.59 | 94.81 | 9.65 | 164.40 | 10.11 | 166.43 |
| | S.D. | 0.82 | 0.34 | 0.70 | 4.18 | 1.95 | 1.24 | 0.48 | 8.46 | 0.54 | 10.82 |
| Lake Timk, Tas. | Mean | 88.22 | 11.95 | 15.31 | 57.84 | 71.91 | 95.11 | 9.24 | 163.86 | 10.40 | 156.91 |
| | S.D. | 0.87 | 0.38 | 1.08 | 4.86 | 1.37 | 1.31 | 0.90 | 12.81 | 0.65 | 9.59 |
| All data | Min. | 84.7 | 11.6 | 10.3 | 50.0 | 69.9 | 89.8 | 7.1 | 138.5 | 8.5 | 136.4 |
| | Mean | 87.46 | 13.82 | 13.22 | 67.21 | 73.85 | 95.01 | 9.85 | 182.17 | 11.10 | 170.42 |
| | Max. | 90.2 | 16.3 | 17.1 | 96.9 | 78.3 | 99.6 | 11.4 | 216.7 | 13.3 | 197.1 |
| New Zealand | Min. | 84.8 | 11.0 | 11.8 | 59.5 | 68.5 | 90.9 | 7.8 | 141.0 | 8.8 | 137.0 |
| | Mean | 87.0 | 13.2 | 13.1 | 71.9 | 73.5 | 95.2 | 9.4 | 176.1 | 10.5 | 162.1 |
| | Max. | 89.3 | 15.3 | 15.8 | 88.5 | 81.3 | 99.0 | 10.8 | 210.1 | 12.2 | 200.0 |

| Pec./PecPel | Pel/Pel. An. | PrePel/S.L. | PecPel/S.L. | Pel An./S.L. | H.L./S.L. | H.W./H.L. | H.D./H.L. | Sn.L./H.L. | P.O.H.L./H.L. | I.D.W./H.L. | E.D./H.L. | L.U.J./H.L. | L.L.J./H.L. | W.G./H.L. | N |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 53.44 | 64.32 | 54.36 | 31.87 | 24.99 | 23.69 | 58.40 | 52.49 | 31.46 | 53.86 | 42.17 | 21.14 | 44.60 | 39.90 | 38.27 | 7 |
| 5.23 | 9.36 | 1.27 | 1.58 | 2.68 | 1.00 | 4.44 | 5.93 | 2.11 | 2.48 | 2.77 | 3.32 | 3.25 | 2.20 | 3.66 | |
| 48.11 | 60.40 | 54.80 | 33.45 | 25.06 | 24.30 | 61.12 | 57.07 | 31.55 | 54.42 | 41.93 | 17.85 | 45.28 | 45.01 | 40.15 | 13 |
| 4.11 | 5.24 | 1.43 | 2.36 | 1.78 | 1.93 | 4.67 | 3.82 | 1.37 | 1.87 | 2.07 | 2.09 | 2.90 | 2.47 | 2.79 | |
| 52.06 | 58.96 | 54.13 | 32.10 | 24.73 | 24.47 | 67.08 | 58.18 | 32.77 | 52.90 | 43.04 | 18.91 | 45.02 | 41.23 | 43.07 | 20 |
| 6.64 | 4.26 | 0.99 | 1.69 | 1.14 | 0.89 | 2.48 | 2.64 | 1.22 | 1.55 | 1.85 | 1.28 | 1.84 | 2.18 | 2.35 | |
| 49.51 | 53.99 | 53.62 | 32.54 | 26.11 | 22.95 | 62.31 | 52.46 | 28.87 | 55.47 | 39.49 | 18.89 | 40.79 | 37.87 | 40.39 | 15 |
| 4.45 | 5.04 | 1.41 | 1.52 | 1.57 | 0.87 | 4.13 | 4.30 | 1.21 | 2.84 | 1.66 | 1.62 | 1.76 | 1.87 | 5.34 | |
| 50.89 | 59.23 | 53.47 | 32.35 | 25.21 | 23.58 | 66.25 | 55.35 | 31.48 | 54.00 | 41.32 | 18.05 | 42.24 | 38.74 | 42.05 | 15 |
| 3.25 | 3.65 | 1.44 | 1.50 | 0.91 | 0.59 | 3.75 | 2.82 | 1.76 | 3.64 | 1.43 | 1.53 | 2.59 | 2.22 | 3.41 | |
| 55.69 | 61.37 | 54.14 | 32.03 | 25.31 | 23.79 | 62.31 | 50.37 | 30.71 | 52.91 | 40.84 | 18.24 | 42.41 | 39.47 | 41.30 | 7 |
| 4.42 | 3.27 | 1.06 | 1.67 | 1.29 | 0.57 | 4.30 | 3.91 | 2.93 | 2.23 | 3.32 | 1.74 | 1.70 | 2.25 | 6.06 | |
| 53.08 | 59.12 | 52.35 | 30.42 | 23.49 | 25.38 | 64.80 | 50.93 | 34.21 | 52.52 | 37.05 | 17.59 | 41.52 | 36.92 | 37.43 | 10 |
| 4.76 | 3.19 | 1.62 | 1.79 | 1.29 | 0.71 | 2.65 | 1.78 | 0.62 | 1.96 | 1.01 | 0.72 | 1.31 | 1.12 | 2.35 | |
| 55.68 | 62.11 | 52.69 | 30.35 | 24.19 | 23.73 | 63.08 | 51.17 | 32.51 | 51.47 | 37.62 | 21.68 | 40.84 | 36.87 | 35.19 | 10 |
| 4.72 | 4.10 | 1.72 | 2.07 | 0.66 | 0.61 | 2.15 | 2.13 | 1.90 | 2.21 | 1.37 | 0.89 | 1.40 | 2.00 | 2.38 | |
| 39.6 | 43.3 | 49.6 | 26.6 | 21.9 | 21.1 | 51.7 | 45.3 | 26.4 | 48.0 | 35.4 | 15.1 | 37.3 | 32.0 | 32.7 | |
| 51.80 | 58.66 | 53.72 | 31.29 | 24.93 | 23.98 | 63.79 | 54.26 | 31.68 | 53.55 | 40.68 | 18.89 | 42.96 | 39.71 | 40.23 | 97 |
| 65.0 | 79.2 | 57.5 | 38.1 | 29.4 | 29.9 | 71.7 | 63.9 | 36.0 | 61.8 | 46.0 | 27.1 | 49.9 | 45.7 | 52.2 | |
| 43.1 | 44.4 | 46.3 | 27.2 | 20.9 | 20.7 | 56.2 | 41.7 | 26.3 | 48.5 | 32.5 | 13.9 | 37.3 | 32.5 | 40.0 | |
| 55.6 | 58.9 | 52.2 | 30.7 | 25.7 | 23.6 | 67.6 | 49.3 | 30.7 | 55.0 | 37.7 | 17.8 | 42.9 | 38.5 | 42.7 | 160 |
| 68.3 | 77.4 | 57.8 | 36.8 | 30.4 | 28.7 | 78.7 | 55.9 | 34.4 | 70.4 | 44.1 | 25.0 | 48.1 | 43.7 | 52.2 | |

habitat disturbance and the combination of rapid waters in bouldery streams of poor accessibility, secretive habits, and sensitivity to disturbance, mean that the fish is not often seen near densely populated areas. It is mostly found in mountainous country — the Blue Mountains, Wilson's Promontory, the Otway Ranges and widely in Tasmania. Andrews (1976: 317) reported that in lakes it is "fairly evenly distributed throughout the body of water", but in streams it is usually benthic, living amongst large rocks or under logs and other cover.

LIFE HISTORY: Little has been reported about the life history of *G. brevipinnis* (papers by Walford, 1928, 1940, 1941, reporting on *G. coxii* are, on the basis of material deposited by him in the Australian Museum, *G. olidus*).

*G. brevipinnis* is well-known to have a marine "whitebait" juvenile in New Zealand, and this has been reported for Tasmania also by Lynch (1965, 1966 — as *G. weedoni*, 1974); in both Tasmania and New Zealand it may form a significant proportion of the whitebait fishery (McDowall and Eldon, In Press). The whitebait juvenile of *G. brevipinnis* was first collected on the Australian mainland by J. Renowden from Browns Creek, Otway Ranges, Victoria on 2 December 1967. Juveniles with patterned pigmentation and of similar size to the Browns Creek whitebait were collected climbing the unlit pit wall of the Mount Ewan storage reservoir by D. D. Lynch (19 November 1959, pers. comm.). The existence of a marine whitebait stage is considered to be a facultative rather than obligatory phase in the life history of *G. brevipinnis*. Populations are known from lakes that are effectively isolated from the sea, e.g. Lake St. Clair and Great Lake in Tasmania and Lake Tali Karng in Victoria. A landlocked population in Lake Eucumbene probably dates from the formation of the lake by a dam across the Snowy River. Similar landlocked populations are numerous in New Zealand (McDowall, 1970a).

Specimens collected at Mossvale (Kangaroo River Valley) on 26 January, 1964 and 8 January, 1976 have immature gonads and a ripe male was taken from Roaring Megs Creek, Wilson's Promontory, in April 1964. A late autumn to early winter spawning season, as in New Zealand (McDowall, 1970a), is therefore likely.

*G. brevipinnis* is well-known for its ability to climb steep water falls and rocky faces. It adheres to the rock surface, out of the water flow, using its ventrally outspread pectoral and pelvic fins. This climbing ability enables it to penetrate great distances inland, moving upstream past formidable barriers. Thus in Rhodes Creek, Flinders Island (Frankenberg 1967), *G. brevipinnis* was recorded upstream from *G. truttaceus* with no overlap in range. An exposed granite incline, fairly steep at the base, apparently acted as a barrier, passable to *G. brevipinnis* but not to *G. truttaceus*.

Nevertheless, *G. brevipinnis* is widely reported in sympatry with *G. truttaceus*, and may occur with *G. maculatus* in more lowland waters. In the upper portions of streams overlap with *G. olidus* has been observed only once — in headwaters of Chapple Creek, Gellibrand River, Victoria. In Great Lake it is also in sympatry with *G. truttaceus* and *Paragalaxias dissimilis* and *P. eleotroides*, in the Julian Lakes, with *G. truttaceus and P. julianus* while Andrews (1976) recorded sympatry with *G. pedderensis* and *G. parvus* in the Serpentine River, Tasmania.

Because *G. brevipinnis* has been recorded so infrequently in the past, usually from only one or two specimens, it is difficult to determine any changes in the distribution and abundance of Australian populations. However, it is becoming increasingly evident that it occurs only in areas inaccessible to trout. Lake Tali Karng, a small high altitude lake in Gippsland, once contained an abundant population of *G. brevipinnis*, but recent expeditions have recorded only brown trout (*Salmo trutta*) from both the lake and a small inflowing stream (Williams, 1964; Frankenberg, 1966a; Timms, 1974). When Lake Eucumbene was formed in 1957, a population of *G. brevipinnis* was trapped and became landlocked, but as the trout population exploded, the population of *G. brevipinnis* has declined and the species is now very rare there (R. D. J. Tilzey, pers. comm.). Andrews (1976:316) reported that in Tasmania *G. brevipinnis* is "abundant in areas which have never been stocked with trout, and also in areas which are protected against invasion, by physical barriers". The same is true in New Zealand (McDowall, 1968d).

DISTRIBUTION: *G. brevipinnis* occurs in Australia, Tasmania, New Zealand, the Chatham Islands, and the Auckland and Campbell Islands. In Australia it is widespread in streams draining east and south from the Great Dividing Range, from the Hunter River in New South Wales, south and west to Kangaroo Island and the Fleuriau Peninsula in South Australia (Fig. 4). It is not known in the Murray-Darling system, nor in drainages into Port Phillip Bay. It is present on Flinders and King Islands in Bass Strait, and is widespread in Tasmania. Published records of *G. truttaceus* from South Australia, e.g. Scott et al. 1974, refer to *G. brevipinnis.*

On the Australian mainland it has apparently failed to become established in the Murray-Darling system, possibly due to the high summer temperatures on the northern and western slopes of the Dividing Range. The physical features of the lower parts of the Murray-Darling system are different from the typical montane habitat of *G. brevipinnis* and there are other competing fish in the system including two galaxiids. The species is also apparently absent from the Port Phillip Bay drainage but because of the proximity of a large city, it is unlikely that this is due to lack of collecting. Possibly suitable streams there have been sufficiently isolated, both by distance and adverse currents, from coastal streams, to limit marine distribution between the mouths of streams. Even at periods in the past when Port Phillip Bay was above sea level drainage conditions were probably of low relief, possibly analogous to the lower parts of the Murray-Darling system at present, and may have represented an unsuitable environment. There are extensive gaps in the known range in Tasmania, especially on the east coast; these gaps may be due to inadequate collecting, but may indicate that the species is poorly represented there.

### **Galaxias olidus** Günther

Fig. 5, 8

*Galaxias olidus* Günther, 1866: 209 (holotype: BMNH 1866.2.13:24, seen; type locality: "?Queensland"); Krefft, 1871: 84; Macleay, 1881a: 46; 1881b: 230; Ogilby, 1886: 54; Regan, 1905: 381; Zietz, 1908: 297; Waite, 1921: 41; McCulloch, 1922: 18; Waite, 1924: 483; McCulloch and Whitley, 1925: 133; Hale, 1928: 25; McCulloch, 1929: 48; Whitley, 1933: 61; 1936: 34; Johnston and Mawson, 1940: 351(?); 1944: 64 (?); 1947: 548 (?); Whitley, 1955: 154; 1956b: 39; Lake, 1971: 20; Andrews, 1973: 105; Pollard, 1974: 117; Grant, 1975: 564; Andrews, 1976: 318; Jackson, 1976: 14; Cadwallader, 1976: 18; Bishop, 1977: 53; Lake, 1978: 24; Fletcher, 1978: 18; Backhouse and Vanner, 1978: 128.

*Galaxias schomburgkii* Peters, 1868: 455 (syntypes: (2) MNUB 6788, seen; type locality; near Adelaide, South Australia); Macleay, 1881: 47; Ogilby, 1896: 69; Regan, 1905: 382; McCulloch, 1929: 49; Stokell, 1947: 671; Whitley, 1956a: 34; 1956b: 39; 1957a: 7; Munro, 1957b: 17; Whitley, 1964: 35; Lake, 1971: 20; Scott, et al., 1974: 78 (new synonymy).

*Galaxias ornatus* Castelnau, 1873: 153 (holotype: MHNH A.5225, not seen; paratype: (1) MHNH A.6915, not seen; type locality: Cardinia Creek, Victoria); Macleay, 1881a: 47; 1881b: 237; Lucas, 1890: 36; Ogilby, 1896: 69; Regan, 1905: 381; Ogilby, 1912: 33;

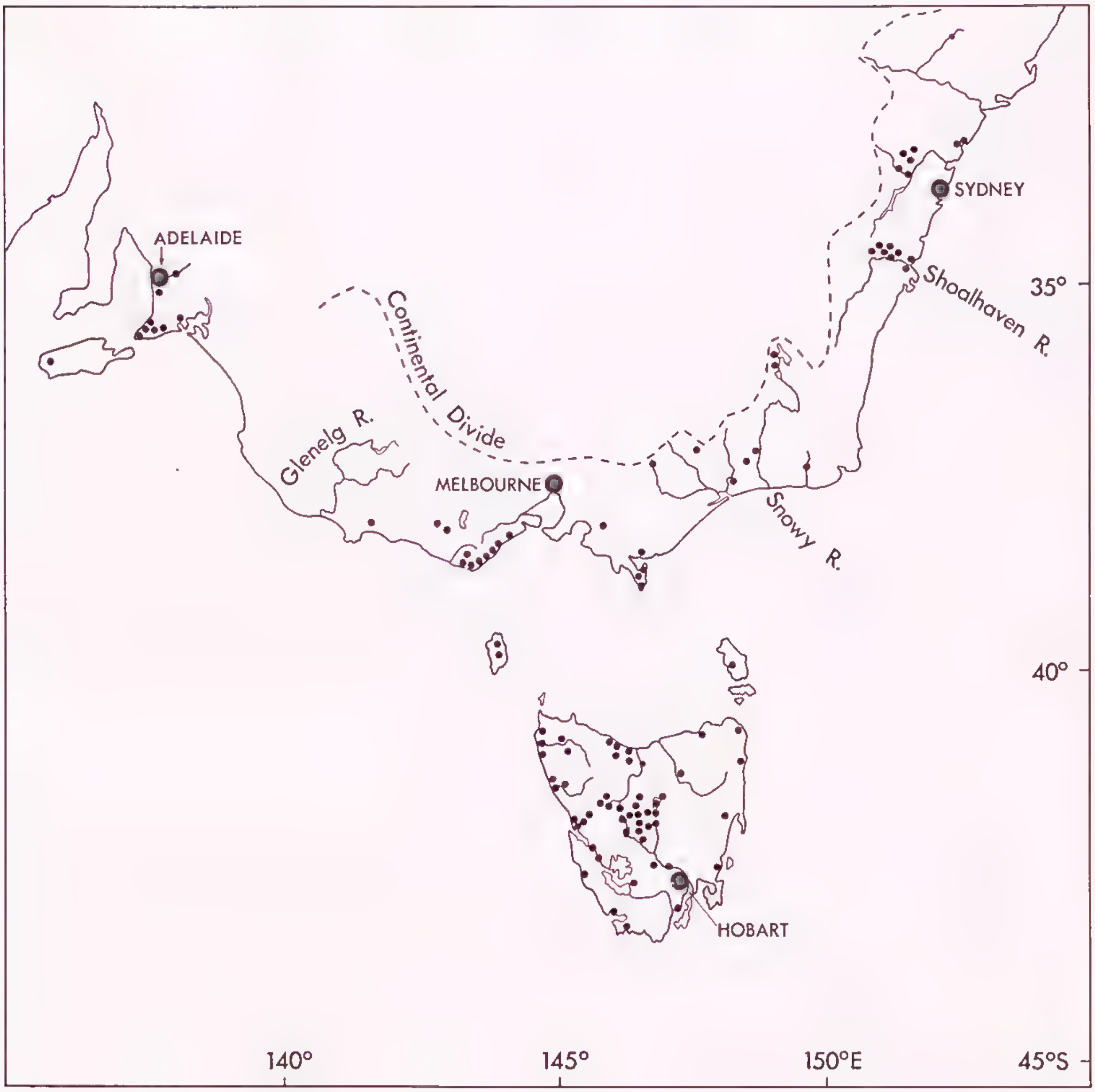

Fig. 4. Distribution of *Galaxias brevipinnis* in Australia. One symbol may represent more than one locality.

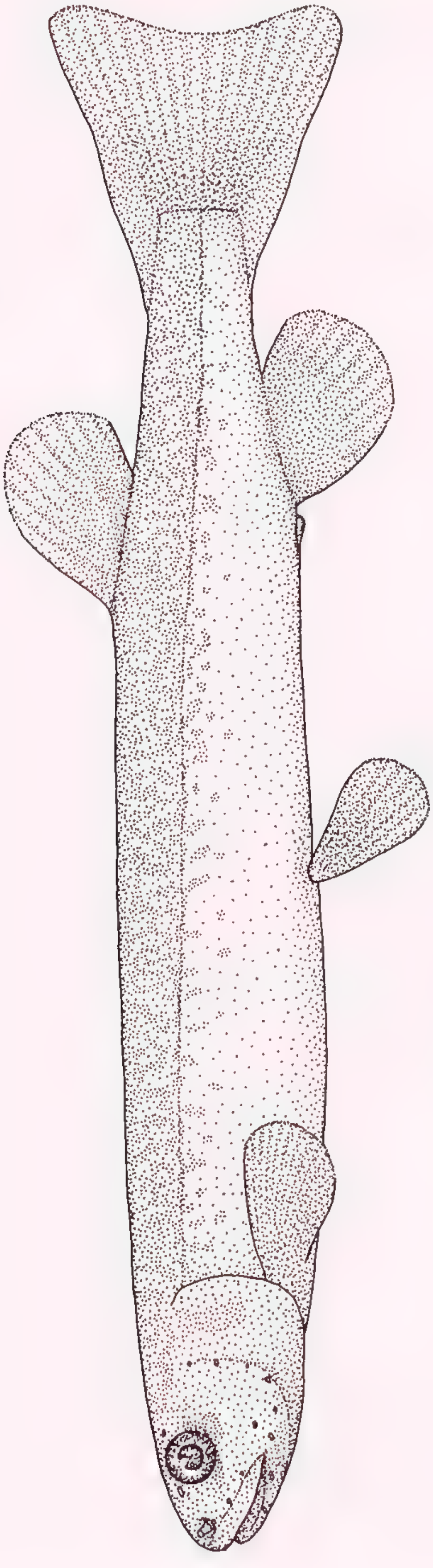

Fig. 5. *Galaxias olidus* Günther; Campbells River, N.S.W., 74 mm L.C.F.

McCulloch, 1929: 48; Whitley, 1934: 268 (partim, incl. *Galaxiella pusilla);* Scott, 1942: 56; Butcher, 1946: 9; Bertin and Esteve, 1951: 3; Whitley, 1955: 154; 1956a: 34; 1956b: 39; 1957a: 7; Munro, 1957b: 17; Frankenberg, 1967: 226; Whitley, 1964: 35; Lake, 1971: 20; Frankenberg, 1971: 95 (new synonymy).

*Galaxias bongbong* Macleay, 1881b: 233 (originally syntypes: (10) MMS F.82; now lectotype: AMS I.16258.002, seen; paralectotypes: (6) AMS I.16258.001, seen; designation, Whitley, 1941; type locality: Mossvale and rivers at Bongbong, New South Wales); Tenison-Woods, 1882: 22; Ogilby, 1886: 55; 1896: 60; Waite, 1904: 17; McCulloch, 1921: 28; 1922: 18; McCulloch and Whitley, 1927: 18; McCulloch, 1929: 49; Whitley, 1934: 268; 1941: 4; 1954: 29; 1956a: 34; 1956b: 39; 1957a: 7; Munro, 1957b: 16; Whitley, 1964: 35; Lake, 1967a: 14; 1967b: 196; Greenham, 1968: 846; Stanbury, 1969: 205; Llewellyn, 1969: 16; 1971: 3; Lake, 1971: 20; Berra, 1973: 363 (new synonymy).

*Galaxias findlayi* Macleay, 1883: 106 (holotype: unknown, probably lost; type locality: Mount Kosciusko); Ogilby, 1886: 55; 1896: 62; Waite, 1904: 17; Regan, 1905: 382; Stead, 1906: 50; McCulloch, 1914: 328; Gale, 1915: 16; McCulloch, 1919: 49; 1921: 28; 1922: 18; 1927: 18; 1929: 49; Tadgell, 1930: 230; Walford, 1940: 234; Stokell, 1945: 124; Costin, 1954: 97; Whitley, 1956a: 34; 1956b: 39; 1957a: 7; Munro, 1957b: 17; Whitley, 1959: 136; Littlejohn, 1962: 311; Whitley, 1964: 35; Tilzey, 1970: 27; Lake, 1971: 20; Thomson, 1974: 151; Baker, 1978: 822 (new synonymy).

*Galaxias kayi* Ramsay and Ogilby, 1887: 6 (syntypes: (5) AMS I.3-7, seen; type locality: Fifth Creek, South Australia); Ogilby, 1896: 69; Stokell, 1945: 25; 1947: 671; Whitley, 1956a: 34; 1957a: 7; 1957b: 57; Munro, 1957b: 17; Scott, 1962: 68; Whitley, 1964: 35; Scott, 1966: 250; Lake, 1971: 20; Scott et al. 1974: 77.

*Galaxias oconnori* Ogilby, 1912: 23 (holotype: QM I.421, seen — a specimen AMS I.11161, described in the AMS catalogue as a "cotype" cannot be a type as Ogilby stated that he had only one specimen; type locality: Lyra, near Stanthorpe); McCulloch and Whitley, 1925: 133; Duhig, 1931: xvi; Whitley, 1956a: 34; 1956b: 39; Munro, 1957b: 17.

*Galaxias coxii* — Walford, 1928: 274; Gray, 1929: 140; Walford, 1940: 234; 1942: 56; Whitley, 1957a: 10 (partim); Garnet, 1959: 213; Breder and Rosen, 1966: 132; Tilzey, 1974: 7 (non *Galaxias coxii* Macleay, 1881).

*Lyragalaxias oconnori* — Whitley, 1935: 42.

*Galaxias fuscus* Mack, 1936: 100 (holotype: NMVM A.96, seen; paratype: (1) NMVM A.99, seen; type locality: Rubicon River, Victoria); Stokell, 1945: 126; Whitley, 1956a: 32; 1956b: 39; 1957a: 7; Munro, 1957b: 17; Whitley, 1964: 35; Lake, 1971: 20; Dixon, 1972: 121 (new synonymy).

TAXONOMY: There has been some controversy over the name *Galaxias olidus* Günther, and its use therefore requires some justification. Stokell (1947) stated that he found it "impossible to identify any fish" with the type specimen on account of the uncertain type locality and abnormalities in the vertebral column that are apparent in a radiograph of the type. Stokell's conclusion is not accepted here. Dr P. H. Greenwood (Curator of Fishes, British Museum (Natural History) ) examined the pyloric caeca of Günther's type in the British Museum and has informed us (pers. comm.) that "I can find only one caecum, a short, broad structure, approximately 5 mm by 3 mm". Such a single, short caecum is known only in the species from the upland-subalpine streams of eastern Australia, and this alone is good evidence of the identity of the fish. A combination of characters in Günther's (1866) description supports this, viz. high pectoral ray count (14), relatively short head (22% of S.L.), lower jaw a little shorter than upper, mouth extending back to almost the middle of eye, small eyes, small pectoral and pelvic fins, and slender caudal peduncle. Regan (1905) redescribed *G. olidus* from the holotype, and additional specimens, including two specimens listed as "types", although Günther had only one fish. Regan's addition of characters such as teeth subequal without distinct canines, maxillary extending to below middle of eye, anal origin behind middle of dorsal, all indicate that the mountain galaxiid here under description is correctly known as *G. olidus*. The only species with which confusion might be possible is *G. brevipinnis* Günther, but this species has two, long pyloric caeca, distinct lateral canines, and much larger pectoral and pelvic fins.

The data suggest that although the holotype has deformities in the vertebral column, and although the type locality is uncertain, the name *G. olidus* is applicable to the eastern Australian mountain galaxiid.

There are two specimens in the jar in the British Museum, labelled as types of *G. olidus*. Stokell (1947) became involved in considering the relation of the second "headless" specimen to the holotype, and he found that it is probably not conspecific with the holotype. However, since Günther (1866) had only one specimen, the second specimen in the jar is not a type and its identity becomes irrelevant.

From examination of a very wide range of specimens from southern Queensland to South Australia, along the mountain ranges, it is our conclusion that none of the seven species listed in the synonymy above is distinct from *G. olidus*. There is a single, rather variable species, variable both in meristic and morphometric characters, and in colouration. Samples from populations throughout the known range of the species have been examined for a wide range of characters, and although there is quite broad variation in some characters there is no indication that more than one species is represented. In no instance is bimodality of characters, which might indicate cryptic species, evident in the data.

Some populations have deviated from the usual seven-rayed pelvic fin of the genus *Galaxias*, to an eight- or even occasionally nine-rayed fin. Eight-rayed pelvic fins appear sporadically in populations from Queensland to South Australia, and this must be seen as mosaic evolution in an already variable species (Table 4).

Synonyms of *G. olidus* are listed above. From an examination of as many of the types as possible, and from study of the original descriptions, it is evident that all these nominal species come within the range of variation of *G. olidus*.

*G. schomburgkii*: The syntypes of *G. schomburgkii* are in good condition, considering their age; however, they are very stiff, preventing fin ray counts being made. Their identity with *G. olidus* is clearly evidenced by the dorsal fin being almost wholly in advance of the anal fin. One of the specimens was opened and the single pyloric caecum also indicates *G. olidus*.

*G. ornatus:* Data from Castelnau's (1873) original description of this species, and from Regan's (1905) redescription of the holotype, are consistent with data presented here for *G. olidus*. The origin of the anal fin is described by Regan as being "slightly in advance of the posterior end of the base of the dorsal", and the short paired fins (pectoral 40% of pectoral-pelvic interval and pelvic 40% of pelvic-anal interval) indicate that *G. ornatus* is a junior synonym of *G. olidus*. The failure of both Castelnau (1873) and Regan (1905) to mention the dark post-pectoral blotch characteristic of and described for the *G. brevipinnis — G. coxii — G. affinis* group by Regan indicates that *G. ornatus* is unlikely to belong to this group of species.

*G. bongbong:* The types of *G. bongbong* — the lectotype and paralectotypes of Whitley (1941) — were examined, and again fall within *G. olidus* as described here, in every respect. The lectotype has one pyloric caecum of moderate length and one that is very short (a not uncommon condition in *G. olidus*), the pectoral fins are very short (36.4% of the pectoral-pelvic interval), and there are no enlarged canine teeth in the jaws.

*G. findlayi:* The types of *G. findlayi* are lost, and the vague type locality which is unspecified other than "captured . . . on Mt Kosciusko", prohibits the collection of material that can be regarded with certainty as topo-typical. Mount Kosciusko drainages flow into both the Snowy (coastal) and Murrumbidgee (inland) drainages. Ogilby (1896) elaborated on Macleay's account and stated that the types came from the Snowy watershed. Ogilby gave the pelvic fin ray count as nine. It is nine very occasionally in *G. olidus* populations with a modal count of eight (Ogilby's material is still in the Australian Museum, and data from his specimens are included in Table 3). Ogilby does not indicate the authority upon which he based his information about the type locality; it may be doubted that he was correct and it may be questioned whether Ogilby's material is truly topotypical. In addition to there being populations in the upper Snowy with eight or more pelvic fin rays, there are also populations with eight rays in the Murrumbidgee, and populations in both systems, in the vicinity of Mt Kosciusko with only seven rays.

Characters described by Macleay, that indicate the identity of his fish as *G. olidus* include pectoral fin less than half pectoral-pelvic interval, pelvic fin less than half pelvic-anal interval, dorsal fin situated almost entirely in front of anal. There are numerous populations of *G. olidus* in the Mt. Kosciusko area which agree with both *G. olidus* and the fish described by Macleay as *G. findlayi.*

*Galaxias kayi: G. kayi* was described from the western extremity of the range of *G. olidus,* in South Australia. Specimens typical of *G. olidus* occur in South Australia as far west as the Mount Lofty Ranges and the types of *G. kayi* agree with these in all general characters. In three of the syntypes examined there is one well-developed pyloric caecum and one short caecum. Ramsay and Ogilby (1886) described the pelvic fin ray count as eight, which is true of only one of the syntypes, the remainder having seven rays, as is typical of most populations of *G. olidus.* We follow Regan (1905) in treating *G. kayi* as a synonym of *G. olidus.*

*G. oconnori:* The holotype of *G. oconnori* has disintegrated almost completely and its characters can no longer be established. *G. olidus* occurs at higher elevations in the hills of southern Queensland, in the vicinity of the type locality, and there is nothing in Ogilby's (1912) description that distinguishes *G. oconnori* from *G. olidus,* as construed here.

*G. fuscus:* As described by Mack (1936) *G. fuscus* differs in no way in its meristic or morphometric characters from *G. olidus* as described here. Mack listed no diagnostic characters, and the only apparent distinctive feature is the presence of "four prominent dark blotches on each side between base of pectoral and origin of dorsal". Colouration in *G. olidus* is highly variable. A sample from the Yea River drainage, near Kinglake, has specimens with very marked vertical dark blotches along the sides, as illustrated for *G. fuscus* by Mack, but there is wide variation in the Yea River fishes — between 0 and 7 such blotches occur and there is no consistency from side to side in any given fish. One fish had seven blotches on one side and two on the other, another had four on one side and none on the other. The significance of this colour pattern and its variation are not understood, but it is regarded as not precluding inclusion of *G. fuscus* in the synonymy of *G. olidus.* Study of a wide range of material suggests a gradation from the barred condition in "*G. fuscus*" to the more usual irregular blotching pattern. The types of *G.*

*fuscus* have become completely dehydrated and are of no use; attempts to obtain topotypical material failed.

The inclusion of references by Walford (1928, 1940, 1941) to *G. coxii* in the synonymy of *G. olidus* is on the basis of material described by Walford as *G. coxii* and deposited in the collections of the Australian Museum. These fish are *G. olidus*. Their identity as *G. olidus*, rather than *G. coxii*, could have been predicted from the life history pattern, with Walford observing the larval fish following hatching, and their growth to maturity in fresh water streams. (Larval growth in *G. brevipinnis* (= *G. coxii*) occurs in fresh water only in landlocked lake populations).

Because of the wide range of material available, and the considerable variability in the characters of *G. olidus*, study was undertaken of the nature of this variation.

Most populations have predominantly seven rays in the pelvic fins, but in a few there are eight rays (Table 3). Eight rays are characteristic of the highest altitude population on the slopes of Mt Kosciusko (Snowy River), but there is no consistent association of eight pelvic rays with altitude, even in the Snowy River. The Native Dog Creek population is eight-rayed, but the Kiandra population at a higher altitude is seven-rayed. Additional eight-rayed populations are widespread from southern Queensland to Victoria in both internal and coastal drainages (Table 3).

Pectoral fin ray counts were found to increase with altitude and as a result regional differences tend to be obscured in comparisons of populations from different river systems. Highest pectoral ray counts occur at Smiggin Holes, near Mt Kosciusko (Snowy River), and the lowest at Scotts Creek, Grampians, western Victoria (Glenelg River), (Table 4a, b).

Dorsal fin ray counts also increased with altitude, but no such trend was found for anal fin rays. Nevertheless in series from similar altitudes in the same region or river system, it was found that dorsal and anal fin ray numbers tend to vary together.

There is wide variation in vertebral numbers, between series. Those at the extreme high and low values may have completely disjunct ranges although there is a complete range of intermediate values. The Mt Kosciusko series is unusual in having a great range (9 vertebrae), but this range may be related, in part, to the very large sample examined (123 counts).

Vertebral number tends to rise with altitude (Fig. 6); however, series from relatively flat but high altitude regions (Bogong, Bennison and Dargo High Plains), provide exceptions, and have counts more typical of lower elevation populations (Fig. 6). Virtually the entire range for the species is represented in samples from the Kiewa River system. Two series from similar and high altitudes, one from a steep locality (56-58 vertebrae) and the other from a relatively flat locality (49-53 vertebrae) have extreme and disjunct values. Each series is from a different branch of the river, the two branches meeting at low altitude (ca. 400 m) where there are populations with intermediate values (52-55 vertebrae).

The relative positions of the dorsal and anal fins were examined by subtracting the predorsal length from the preanal length and dividing this difference by the length of the dorsal fin base (PreA. — PreD./L.D.B.). Values for this ratio show an increase with altitude, i.e. the anal fin becomes relatively more posterior with respect to the dorsal fin (Fig. 7). Nevertheless there is considerable variation, particularly between lowland populations.

Table 3. Variation in pelvic fin ray number in *Galaxias olidus*.
Listed in order of increasing mean value.

| | 6 | 7 | 8 | 9 | Mean |
|---|---|---|---|---|---|
| Near Major Ck, Shoalhaven R, NSW | 1 | 6 | | | 6.86 |
| Parker R, Vic | 1 | 6 | | | 6.86 |
| First Ck, nr Adelaide, SA | 1 | 24 | | | 6.96 |
| Seymour Ck, Otways, Vic | | 10 | | | 7.00 |
| Macquarie Rivulet, Shoalhaven R, NSW | | 10 | | | 7.00 |
| Accommodation Ck, Severn R, NSW | | 10 | | | 7.00 |
| Mountain Ck, nr Kinglake, Goulburn R, NSW | | 10 | | | 7.00 |
| Dundurrabin, Clarence R, NSW | | 4 | | | 7.00 |
| Cordeaux R, Hawkesbury R, NSW | | 18 | | | 7.00 |
| Near Delegate, Snowy R, NSW | | 8 | | | 7.00 |
| Near Kiandra, Snowy R, NSW | | 25 | | | 7.00 |
| Bennison High Plains, Vic | | 13 | | | 7.00 |
| Jeeralong Ck, Latrobe R, Vic | | 6 | | | 7.00 |
| Chapple and Charlies Cks, Gellibrand R, Vic | | 15 | | | 7.00 |
| Scott Ck, Glenelg R, Vic | | 9 | | | 7.00 |
| Bogong High Plains, Vic | | 24 | 1 | | 7.04 |
| Glen Stuart, SA | | 14 | 1 | | 7.07 |
| Clearwater Ck, Port Phillip, Vic | | 11 | 1 | | 7.08 |
| Ann R. NSW | | 9 | 1 | | 7.10 |
| Megalong Ck, Katoomba, NSW | | 9 | 1 | | 7.10 |
| Bells Ck, Moruya R, NSW | | 7 | 1 | | 7.13 |
| Condobolin, NSW | | 6 | 1 | | 7.14 |
| Fifth Creek, SA | | 5 | 1 | | 7.17 |
| Lake George, NSW | | 9 | 2 | | 7.18 |
| Myponga R | | 4 | 1 | | 7.20 |
| Belair National Park | | 12 | 3 | 1 | 7.31 |
| Wallangara, Qld | | 4 | 2 | | 7.33 |
| West Branch, Kiewa R | | 5 | 3 | | 7.38 |
| Canobolas | | 8 | 2 | | 7.20 |
| Goomburra District, Qld | | 8 | 6 | | 7.43 |
| Crooked Ck, E. of Tenterfield, NSW | | 5 | 5 | | 7.50 |
| Wallaby Ck, Clarence R, NSW | | 2 | 4 | | 7.67 |
| Tooma R tributary, NSW | | 4 | 11 | | 7.73 |
| Running Ck, Kiewa R, Vic | | 1 | 3 | | 7.75 |
| Headwaters Buchan R, Vic | | 3 | 9 | | 7.75 |
| Woody Yallock R, Vic | | 1 | 3 | | 7.75 |
| Four Mile Creek, NSW? | | 6 | 19 | | 7.76 |
| Tributary Tumut R, NSW | | 2 | 8 | | 7.80 |
| Snowy River Pools, Vic | | 3 | 22 | | 7.88 |
| Smiggin Holes, Mt Kosciusko, NSW | | 1 | 24 | | 7.96 |
| Warwick, Qld | | | 4 | | 8.00 |
| Blue Lake, Mt Kosciusko, NSW | | | 5 | 3 | 8.38 |
| Mt Kosciusko, NSW | | | 3 | 2 | 8.40 |

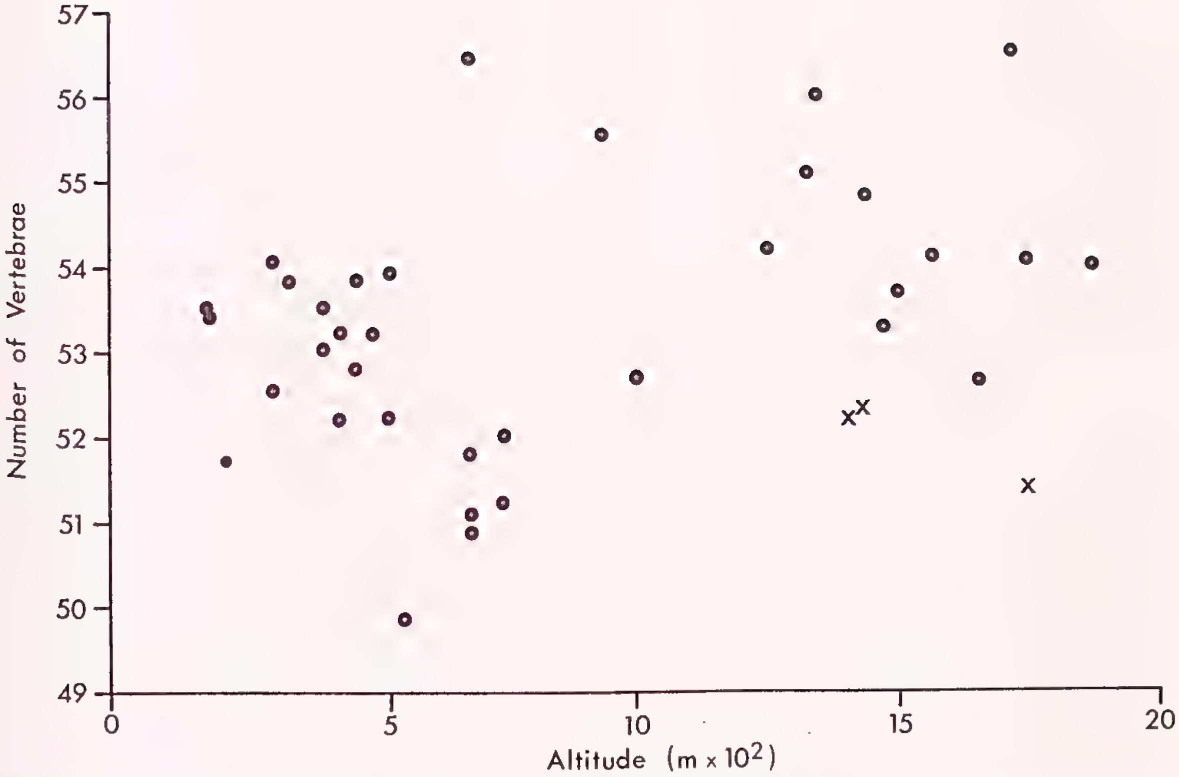

Fig. 6. Variation with altitude in the number of vertebrae in *Galaxias olidus* (crosses indicate populations on high altitude plateaux).

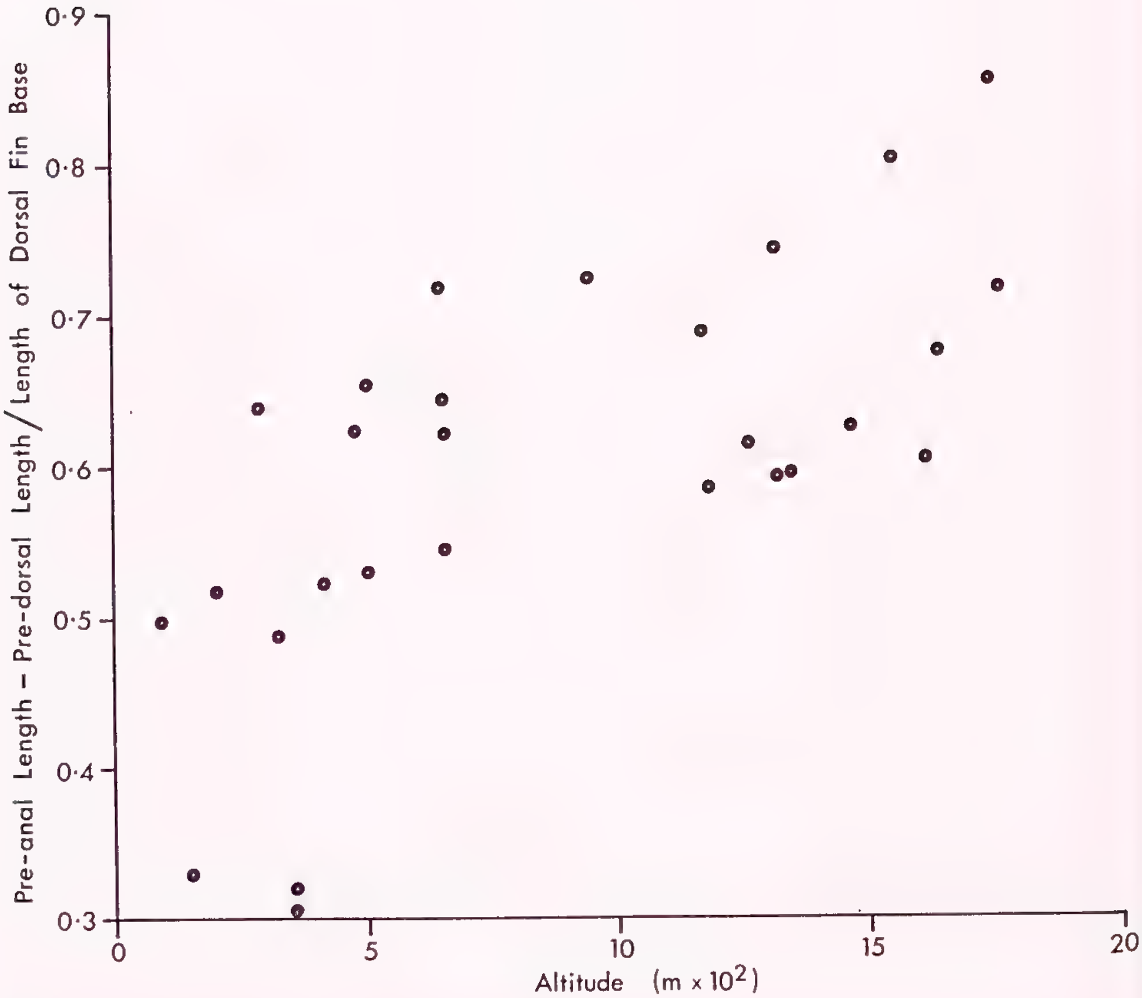

Fig. 7. Variation with altitude in the relative positions of the dorsal and anal fins in *Galaxias olidus*.

In Murray River tributaries at low altitudes there is a high degree of concordance over a fairly wide geographical range between series from the Wimmera, Loddon, Campaspe, Ovens and Kiewa Rivers, and to a slightly lesser extent, the Woady Yallock River (internal drainage to Lake Carangamite). The characteristic features of this group include the fact that the pyloric caeca are vestigial or absent (except Wooragee), the difference between the dorsal and anal fin ray counts is relatively high, and the anal fin usually originates anterior to the mid-point of the dorsal fin base (about under the mid-point in the Loddon and Campaspe River series). This group, however, differs to no great extent from series from the Murrumbidgee basin at low altitudes and southern Victorian coastal rivers, in which there is generally less difference between the dorsal and anal fin ray counts; also southern Victorian fish tend to have relatively more barred colour pattern, and in Murrumbidgee fish the anal fin is relatively more posterior with respect to the dorsal fin.

The only other morphological-geographical groups which can be established occur within large river systems and are associated with the *"fuscus"* and *"findlayi"* colour patterns. The *fuscus* colour pattern in its typical form (bold vertical bars, variable in number) is restricted to two series of fish (Rubicon and Yea Rivers) from the Goulburn River basin, and occasional specimens from the adjacent Ovens River. A somewhat intermediate stage in the development of the *fuscus* pattern occurs in the Ovens River, a tributary of the Murray River near Walwa, and is represented by narrower and more numerous vertical bars. Outside these rivers the pattern is not recognisable. The *findlayi* pattern is represented by a series of dark, irregular blotches, but this pattern grades into the more typical speckled or vermiculated pattern; it is typical of some populations in the upper Snowy and Buchan Rivers.

Certain populations have characteristics which set them apart from most others, and each of these can often be associated with a high degree of isolation and/or peculiarities in the physical environment. The population in Snobs Creek for instance, is located above a waterfall about 26 m high, in a continuously flowing stream with virtually no still pools or backwaters. This population is characterised by high fin ray and vertebral counts. The Dargo High Plains sample was collected from a relatively high altitude lava plain and the fish tended to be uniformly melanistic on the back and upper sides, and lack any form of colour pattern.

DIAGNOSIS: Characterised by anal fin origin usually being below or behind the middle of the dorsal fin, small pectoral and pelvic fins, small eye, and, very often, only a single pyloric caecum.

Differs from *G. brevipinnis* in characters listed in the diagnosis of that species (p.462). Differs from *G. johnstoni* in often having only a single pyloric caecum, more pectoral fin rays, shorter pelvic fins, and usually a somewhat shorter head. Differs from *G. pedderensis* in being generally stouter in build, and in having more pectoral fin rays, shorter pelvic fins, and usually a somewhat shorter head. Lateral pigmentation tends to become fragmented below the lateral line in *G. pedderensis* but not in *G. olidus*. Differences between *G. olidus*, *G. johnstoni* and *G. pedderensis* are relatively slight and the three species appear to be closely related. Differs from *G. fontanus* in lacking lateral canine teeth, in having one pyloric caecum and only four pores in the row below the eyes.

DESCRIPTION: A smallish, and variable but moderately stout species. Trunk rounded in section, often with the belly deepened, dorsal and ventral trunk profiles only slightly and evenly arched, tapering anteriorly to a blunt snout, and posteriorly to a long and slender caudal peduncle, the peduncle much longer than deep. Head short, somewhat flattened dorsally, much broader than deep; snout of moderate length, bluntly rounded, broad. Mouth slightly oblique, large, reaching back well below eyes;

jaws subequal, lower sometimes a little shorter than upper. Eyes small, deep in lateral head, interorbital convex but flattened dorsally. Jaws with little or no enlargement of canine teeth laterally; mesopterygoidal and lingual teeth well developed. Gill rakers short and stout (Fig. 43); pyloric caeca variable, usually one short caecum, but sometimes none, occasionally two (Fig. 45). Laterosensory pores on head as in Fig. 47.

Fins small, thick and fleshy at bases; dorsal and anal fins short-based and rounded, hindmost rays of moderate length. Anal fin origin below middle of dorsal fin base or further back, sometimes below rear of dorsal. Pectoral fins small and paddle-shaped, inserted low lateroventrally, with lamina of fin often facing ventrally. Pelvic fins also small, inserted at or a little behind mid-point of standard length. Caudal fin weakly forked to truncate, fin tips rounded; fin depth about equal to body depth. Caudal peduncle flanges well developed.

Variation: meristic: see Table 4a, b.
morphometric: see Table 5.

COLOUR: Colour of *G. olidus* is widely variable (Fig. 8). When alive it is variably yellowish-green through brown, the belly lighter olive to whitish. The back and upper sides and the head are variably and profusely covered with darker grey-olive speckling, spotting, blotching or banding. The fins are transluscent and olive-gold to greyish and the eyes silvery-olive.

In preservative it is grey-white to brownish-olive on the back with patterning, in its generalised form, consisting of irregular bars or fasciae of various widths which tend to become more irregular and broken dorsally. In the caudal region, in particular, the bars may be chevron-shaped, following the myomeres, but in general the chevron pattern is never very prominent, and may be overlaid on the flanks by a more constrasting pattern bearing no relation to the myomeres. Lateral pigment pattern is very often restricted to the area of the side above the lateral line, any pigmentation below the lateral line often being very pale.

An unusual pattern characterises fish described by Mack (1936) as *G. fuscus,* and observed in fish from a tributary of the Yea River (Goulburn River basin). In these series varying numbers of dark, vertical, and somewhat ovoid bars occur along the flanks anterior to the dorsal fin. In certain series from the adjacent Ovens River basin, (a tributary of the Murray River near Walwa) a pattern of prominent vertical bands also occurs along the flanks, but these are narrower and more closely spaced than in the typical *"fuscus"* pattern, and are also more evenly distributed along the length of the fish. In some other series there is a tendency for markings along the lateral line to be accentuated, but not as prominently as in the above-mentioned Goulburn and Ovens River fishes. There is therefore a gradation from the typical *"fuscus"* pattern to the more generalised pattern.

A pattern of dark irregular blotches is characteristic of series from the upper Snowy and Buchan Rivers, although in a number of Snowy River specimens (Smiggin Holes), scarcely any pattern is developed. Pattern is also essentially lacking in series from Snobs Creek, the Wimmera River and Dargo High Plains; the last mentioned is characterised by a very dark-coloured upper body.

Chevron-shaped, but somewhat indistinct bars are often evident in fish from southern Victoria, but in southwestern Victoria and much of the Murray-Darling basin a finer more marbled or fasciated pattern is characteristic.

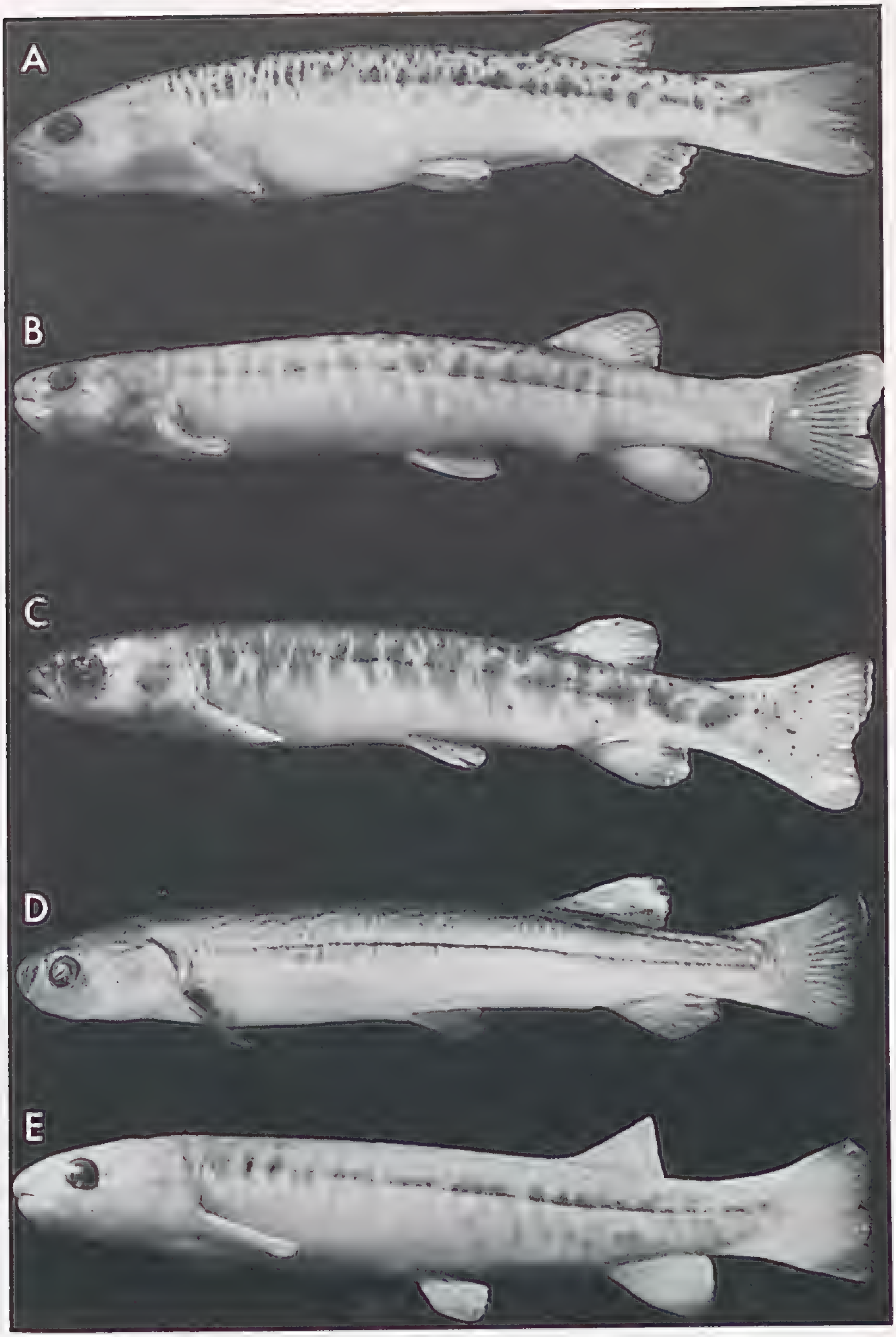

Fig. 8. Variation in colour pattern in *Galaxias olidus;* **a.** Swanbrook Creek, N.S.W., 58 mm L.C.F.; **b.** Watchbox Creek, Vic., 64 mm L.C.F.; **c.** Running Creek, Kinglake, Vic., 67.5 mm L.C.F.; **d.** Campbell River, N.S.W., 74 mm L.C.F.; **e.** Macquarie Rivulet, N.S.W., 70 mm L.C.F.

Table 4a. Meristic variation in *Galaxias olidus* (coastal drainages).

| | | Dundurrabin Clarence R., N.S.W. | Cordeaux Ck Hawkesbury R., N.S.W. | Macquarie Rivulet Shoalhaven R., N.S.W. | N. Majors Ck Shoalhaven R., N.S.W. | Bells Ck Moruya R., N.S.W. | nr. Delegate Snowy R., N.S.W. | Near Kiandra Snowy R., N.S.W. | Smiggin Holes Snowy R., N.S.W. | Mt Kosciusko Snowy R., N.S.W. | Native Dog Ck Snowy R., N.S.W. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Dorsal rays — segmented | 8 | | | 1 | | | | | | | |
| | 9 | | | 4 | | | | | | | 1 |
| | 10 | | | 4 | | | | | | | 1 |
| | 11 | | | 8 | | | | | | | 8 |
| | 12 | | | | | | | | | | |
| total | 10 | | | | | | | | | | |
| | 11 | | 1 | 4 | | 2 | 1 | 1 | | | |
| | 12 | | 2 | 5 | 3 | 4 | 3 | 16 | 1 | | |
| | 13 | 1 | 12 | 1 | 4 | 2 | 3 | 8 | 6 | 2 | 1 |
| | 14 | 3 | 3 | | | | 1 | | 5 | 13 | 8 |
| | 15 | | | | | | | | 4 | 9 | 2 |
| | 16 | | | | | | | | 1 | 1 | 0 |
| | 17 | | | | | | | | | | 1 |
| Anal rays — segmented | 9 | | | 1 | | | | | | | |
| | 10 | | | 5 | | | | | | | |
| | 11 | | | 4 | | | | | | | 2 |
| | 12 | | | | | | | | | | 7 |
| | 13 | | | | | | | | | | 1 |
| total | 11 | | | | | | | | | | |
| | 12 | | | 5 | | 1 | | | | | |
| | 13 | 1 | 1 | 3 | 3 | 3 | 1 | | 2 | 3 | |
| | 14 | 2 | 5 | 2 | 2 | 3 | 3 | 13 | 10 | 8 | 1 |
| | 15 | 1 | 11 | | 2 | 1 | 3 | 10 | 4 | 11 | 5 |
| | 16 | | 1 | | | | 1 | 2 | 1 | 3 | 6 |
| Pectoral rays | 12 | | | | | | | | | | |
| | 13 | 1 | 2 | 4 | | 2 | 1 | | | 1 | |
| | 14 | 2 | 14 | 5 | 4 | 5 | 5 | 1 | | 1 | |
| | 15 | 1 | 2 | 1 | 3 | 1 | 2 | 9 | 2 | 7 | 6 |
| | 16 | | | | | | | 13 | 4 | 16 | 4 |
| | 17 | | | | | | | 2 | 9 | | 2 |
| | 18 | | | | | | | | 2 | | |
| Gill rakers | 11 | | | 2 | | | | | | | 1 |
| | 12 | | | 7 | | | | | | | 6 |
| | 13 | | | 1 | | | | | | | 2 |
| | 14 | | | | | | | | | | 1 |
| Vertebrae | 49 | | 1 | | 1 | 3 | | | | | |
| | 50 | | 4 | | 7 | 3 | 5 | | | | |
| | 51 | | 13 | 4 | 7 | 2 | 7 | | | 2 | |
| | 52 | 1 | 5 | 10 | 7 | | 9 | 3 | 1 | 8 | |
| | 53 | 1 | 2 | | 2 | | 3 | 7 | 4 | 42 | 2 |
| | 54 | | | | 1 | | | 11 | 10 | 37 | 7 |
| | 55 | | | | | | | 3 | 2 | 14 | 1 |
| | 56 | | | | | | | 1 | 3 | 10 | 0 |
| | 57 | | | | | | | | | 6 | 1 |
| | 58 | | | | | | | | | 3 | |
| | 59 | | | | | | | | | 1 | |

| Dargo High Plains Mitchell R., Vic. | Bennison High Plains MacAlister R., Vic. | Jerralong Ck Latrobe R., Vic. | Clearwater Ck Pt Phillip, Vic. | Parker R., Vic. | Chapple & Charlies Cks Gellibrand R., Vic. | Seymour Ck Otways, Vic. | Scotts Ck Glenelg R. Grampians, Vic. | First Ck S.A. | Myponga R., S.A. | Fifth Ck S.A. | Glen Stuart S.A. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 1 | | | | | 1 |
| | | | | | | 5 | | | | 1 | 8 |
| | | | | | | 4 | | | | 4 | 6 |
| | | | | | | | | | | 1 | |
| | | | | | | | | | | | |
| | | | | | | | | | | | 1 |
| | 3 | | 2 | 1 | | 4 | | 1 | | 1 | 1 |
| 12 | 5 | | 6 | 6 | 4 | 4 | 7 | 6 | 5 | 1 | 11 |
| 12 | 5 | | 4 | | 10 | 2 | 2 | 15 | | 4 | 2 |
| 1 | | 3 | | | 1 | | | 3 | | | |
| | | 3 | | | | | | | | | |
| | | | | | | | | | | | |
| | | | | | | | | | | | |
| | | | | | | | | | | | |
| | | | | | | 2 | | | | 6 | 9 |
| | | | | | | 7 | | | | | 6 |
| | | | | | | 1 | | | | | |
| | | | | | | | | | | | |
| | | | | | | | | | | | |
| 1 | | | | | | | | | | 1 | 1 |
| 8 | 5 | | | | | 3 | | 5 | 1 | 4 | 4 |
| 13 | 7 | | 3 | 4 | 2 | 6 | 5 | 16 | 4 | 1 | 9 |
| 3 | 1 | 4 | 9 | 3 | 7 | 1 | 3 | 4 | | | 0 |
| | | 2 | | | 6 | | 1 | | | | 6 |
| | | | | | | | | | | | |
| | | 1 | | | | 2 | 4 | | | | |
| | 4 | 2 | | 4 | 3 | 6 | 5 | 12 | | 3 | 4 |
| 12 | 6 | 2 | 4 | 2 | 6 | 2 | | 10 | | 2 | 9 |
| 12 | 2 | 1 | 6 | 1 | 6 | | | 3 | 3 | 1 | 2 |
| 1 | 1 | | 2 | | | | | | 2 | | |
| | | | | | | | | | | | |
| | | | | | | 5 | | | | | 1 |
| | | | | | | 5 | | | | 4 | 11 |
| | | | | | | | | | | 2 | 3 |
| | | | | | | | | | | | |
| | | | | | | | | | 1 | | |
| | | | | 1 | | | | | 1 | | |
| 4 | 3 | | 4 | 1 | 3 | | 3 | 3 | 3 | | |
| 12 | 4 | | 14 | 4 | 4 | | 6 | 12 | | | |
| 9 | 5 | 3 | 6 | 1 | 5 | | | 9 | | | |
| | 1 | 3 | 1 | | | | | 1 | | | |
| | | | | | | | | | | | |
| | | | | | | | | | | | |
| | | | | | | | | | | | |
| | | | | | | | | | | | |
| | | | | | | | | | | | |

Table 4b. Meristic variation in *Galaxias olidus* (inland drainages).

| | | Condamine R. Warwick, Qld. | Crooked Ck E. of Tenterfield, N.S.W. | Accommodation Ck Severn R., N.S.W. | Ann R., N.S.W. | Condobolin, N.S.W. | Canobolas, N.S.W. | Megalong Ck Katoomba, N.S.W. | Towney's Ck Molonglo R., N.S.W. | Burra Ck Queenbeyan R., N.S.W. | 30 km S. of Rules Point Goodradigbee R., N.S.W. | Happy Jacks Ck Tumut R., N.S.W. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dorsal rays — segmented | 8 | | | | | | 1 | | | | | 1 |
| | 9 | | | 4 | | 3 | 5 | 3 | | | | 6 |
| | 10 | | 2 | 3 | 8 | 4 | 4 | 7 | | | | 2 |
| | 11 | | 7 | 4 | 2 | | | | | | | 1 |
| | 12 | | 1 | | | | | | | | | |
| total | 10 | | | | | | | | | 1 | | |
| | 11 | 1 | | 2 | | | 3 | | 1 | 0 | | |
| | 12 | 3 | | 2 | | 2 | 5 | 2 | 9 | 3 | | 3 |
| | 13 | | 4 | 3 | 5 | 5 | 2 | 7 | 2 | 8 | 6 | 13 |
| | 14 | | 5 | 3 | 4 | | | 1 | | 3 | 9 | 7 |
| | 15 | | 1 | | 1 | | | | | 3 | 3 | 2 |
| | 16 | | | | | | | | | | | |
| | 17 | | | | | | | | | | | |
| Anal rays —segmented | 9 | | | | | | 1 | 1 | | | | |
| | 10 | | | | 4 | 5 | 5 | 4 | | | | 1 |
| | 11 | | 5 | 10 | 5 | 2 | 4 | 5 | | | | 9 |
| | 12 | | 4 | | 1 | | | | | | | |
| | 13 | | 1 | | | | | | | | | |
| total | 11 | | | | | | | | | | | |
| | 12 | | | | 1 | | | 1 | | | | |
| | 13 | 1 | 4 | 4 | 2 | 5 | 6 | 2 | 1 | 1 | 2 | 1 |
| | 14 | 2 | 3 | 5 | 3 | 1 | 4 | 7 | 6 | 5 | 7 | 9 |
| | 15 | 1 | 3 | 1 | 4 | 1 | | | 5 | 6 | 7 | |
| | 16 | | | | | | | | | 3 | 1 | |
| | 17 | | | | | | | | | | 1 | |
| Pectoral rays | 11 | | | | | | | | | | | |
| | 12 | | | | | | | | | | | |
| | 13 | 1 | | 1 | | | | 1 | | | | 2 |
| | 14 | 2 | 4 | 5 | 3 | 2 | 1 | 6 | | 2 | | 5 |
| | 15 | 1 | 6 | 2 | 5 | 3 | 8 | 2 | 4 | 4 | | 11 |
| | 16 | | | 1 | 1 | 2 | 1 | 1 | 7 | 8 | 8 | 6 |
| | 17 | | | | | | | | 1 | 1 | 7 | 1 |
| | 18 | | | | | | | | | | 3 | |
| Gill rakers | 10 | | | | | | | | | | | |
| | 11 | | | | | | | | | | | 1 |
| | 12 | | 4 | | 2 | 2 | 2 | | | | | 8 |
| | 13 | | 2 | 4 | 5 | 3 | 6 | 5 | | | | 1 |
| | 14 | | 4 | 3 | 3 | 1 | 2 | 5 | | | | |
| | 15 | | | 3 | | 1 | | | | | | |
| Vertebrae | 49 | | | | | | | | | | | |
| | 50 | | | | | | | | | | | |
| | 51 | 3 | | | | | | | 2 | 5 | | 3 |
| | 52 | 1 | | | | | | | 4 | 8 | | 3 |
| | 53 | | | | | | | | 3 | 2 | 2 | 8 |
| | 54 | | | | | | | | 2 | | 10 | 8 |
| | 55 | | | | | | | | 1 | | 6 | 1 |
| | 56 | | | | | | | | | | 5 | 2 |
| | 57 | | | | | | | | | | 2 | |
| | 58 | | | | | | | | | | | |
| | 59 | | | | | | | | | | | |

| West Branch Kiewa R. | Lake George, A.C.T. | Cobungra R. Mitta Mitta Syst. | Middle Ck Mitta Mitta Syst. | Pretty Valley Kiewa R., Vic. | Yackadandah Ck Kiewa R., Vic. | Mt Buffalo Ovens R., Vic. | 27 km S.E. of Wangaratta Ovens R., Vic. | Scrubby Ck nr Alexandra Goulburn R., Vic. | Mountain Ck nr Kinglake Goulburn R., Vic. | Strath Ck Goulburn R., Vic. | Seven Cks Goulburn R., Vic. | Near Tooboree Campaspe R., Vic. | Blackjack and Barkers Cks Loddon R., Vic. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | 1 | | |
| | | | | | | | | | 2 | | 5 | | |
| | | | | | | | | | 6 | | 4 | | |
| | | | | | | | | | 2 | | | | |
| | | | | | | | | | | | | | |
| | | | | | | | | | | | | | |
| | 4 | | | | | | 6 | | | | 6 | 2 | 6 |
| 1 | 4 | 1 | 1 | 1 | 8 | 3 | 6 | 5 | 9 | 4 | 3 | 8 | 6 |
| 1 | 3 | 6 | 9 | 6 | 1 | 12 | 2 | 9 | 14 | 19 | 1 | 3 | |
| 6 | | 2 | 1 | 5 | | 8 | | 11 | 2 | 2 | | | |
| | | | | 4 | | 0 | | | | | | | |
| | | | | 1 | | 2 | | | | | | | |
| | | | | | | | | | | | | | |
| | | | | | | | | | | | | | |
| | | | | | | | | | 1 | | | | |
| | | | | | | | | | 5 | | 2 | | |
| | | | | | | | | | 4 | | 6 | | |
| | | | | | | | | | | | 2 | | |
| | | | | | | | | | | | | | |
| | | | | | | | | | | | | | |
| | 3 | | 2 | 5 | | 5 | | | 4 | 2 | | | |
| 4 | 5 | 4 | 8 | 8 | 2 | 13 | 3 | 4 | 2 | 7 | 2 | 2 | 1 |
| 3 | 3 | 3 | 0 | 4 | 2 | 7 | 9 | 14 | 4 | 15 | 7 | 2 | 7 |
| 2 | | 2 | 1 | | 4 | | 2 | 6 | | 1 | 1 | 6 | 4 |
| | | | | | 1 | | | 1 | | | | 3 | |
| | | | | | | | | | | | | | |
| | | | | | | | | | | | | | |
| | | | | | | 1 | | | | | | 2 | 1 |
| | 4 | | 1 | 2 | 4 | 3 | 6 | 2 | | 6 | 8 | 9 | 6 |
| 2 | 5 | 3 | 4 | 6 | 5 | 12 | 8 | 8 | 2 | 13 | 2 | 2 | 5 |
| 5 | 2 | 5 | 4 | 6 | | 9 | | 9 | 17 | 6 | | | |
| 3 | | 1 | | 3 | | | | 6 | 6 | | | | |
| | | | | | | | | | | | | | |
| | | | | | | | | | | | 1 | | |
| | | | | | | | | | 1 | | 2 | | |
| | | | | | | | | | 1 | | 3 | | |
| | | | | | | | | | 5 | | 3 | | |
| | | | | | | | | | 3 | | 1 | | |
| | | | | | | | | | | | | | |
| | | | | 1 | | | | | | | | | |
| | 3 | | | 3 | | | | | | | | | |
| | 6 | | 1 | 10 | | | | 1 | | | | | |
| | 0 | | 4 | 7 | 4 | 1 | 3 | 1 | 2 | 7 | | | 2 |
| | 1 | | 4 | 4 | 10 | 4 | 5 | 5 | 18 | 11 | | 4 | 0 |
| | | | 1 | | 6 | 14 | 4 | 12 | 5 | 3 | | 5 | 9 |
| | | | 1 | | 4 | 4 | 2 | 5 | | 4 | | 4 | 1 |
| 5 | | | | | 1 | 2 | | 1 | | | | | |
| 2 | | | | | | | | | | | | | |
| 1 | | | | | | | | | | | | | |
| | | | | | | | | | | | | | |

Table 5. Morphometric variation in *Galaxias olidus*.
Figures are given as percentages of denominators in ratios.

| | | S.L./T.L. | B.D.V./S.L. | L.C.P./S.L. | D.C.P./L.C.P. | Pre D./S.L. | Pre D./Pre A. | L.D.B./ S.L. | M.L.D./ L.D.B. | L.A.B./ S.L. | M.L.A./ L.A.B. | Pec./ Pec. Pel. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tenterfield | Mean | 88.30 | 12.43 | 14.35 | 64.32 | 69.78 | 91.70 | 11.33 | 152.18 | 11.34 | 145.06 | 46.40 |
| N.S.W. | S.D. | 0.80 | 0.50 | 0.54 | 3.00 | 1.14 | 2.64 | 0.64 | 12.37 | 0.58 | 11.67 | 3.11 |
| Ann R. | Mean | 88.99 | 12.02 | 14.37 | 56.45 | 69.55 | 92.64 | 10.79 | 150.74 | 11.62 | 143.84 | 44.51 |
| N.S.W. | S.D. | 0.79 | 1.26 | 0.97 | 4.34 | 0.95 | 1.01 | 0.74 | 10.54 | 0.58 | 6.74 | 3.65 |
| Severn R. | Mean | 89.97 | 11.83 | 12.82 | 72.03 | 72.34 | 91.66 | 10.06 | 156.53 | 10.00 | 164.56 | 40.46 |
| N.S.W. | S.D. | 2.57 | 0.71 | 0.53 | 4.25 | 1.03 | 1.19 | 0.97 | 20.36 | 0.65 | 7.22 | 4.43 |
| Canobolas | Mean | 89.23 | 12.22 | 13.84 | 62.77 | 70.41 | 92.63 | 9.49 | 161.32 | 10.53 | 155.02 | 41.71 |
| N.S.W. | S.D. | 1.01 | 0.75 | 0.48 | 5.41 | 1.43 | 2.12 | 0.82 | 12.01 | 0.61 | 8.53 | 2.69 |
| Condobolin | Mean | 89.56 | 11.33 | 13.46 | 58.41 | 69.58 | 90.96 | 9.81 | 146.81 | 10.58 | 142.53 | 36.31 |
| N.S.W. | S.D. | 1.48 | 0.48 | 0.40 | 3.32 | 1.64 | 1.82 | 1.16 | 14.38 | 1.34 | 10.04 | 6.88 |
| Katoomba | Mean | 88.90 | 11.31 | 14.97 | 57.74 | 68.25 | 91.59 | 10.42 | 163.39 | 10.67 | 157.72 | 46.73 |
| N.S.W. | S.D. | 1.07 | 0.91 | 0.78 | 5.02 | 1.23 | 2.31 | 0.84 | 10.85 | 0.89 | 7.43 | 2.65 |
| Macquarie Rivulet | Mean | 89.39 | 13.68 | 13.94 | 70.34 | 71.51 | 92.96 | 9.23 | 158.59 | 10.23 | 154.83 | 37.80 |
| N.S.W. | S.D. | 0.99 | 0.94 | 1.14 | 6.64 | 1.50 | 1.32 | 0.66 | 13.38 | 0.49 | 8.81 | 5.65 |
| Seven Creeks | Mean | 88.82 | 13.11 | 14.08 | 59.08 | 69.42 | 94.01 | 8.90 | 171.99 | 12.36 | 140.25 | 40.92 |
| N.S.W. | S.D. | 0.70 | 1.08 | 0.52 | 3.27 | 2.98 | 1.17 | 0.64 | 8.32 | 0.80 | 3.73 | 2.62 |
| Native Dog Creek | Mean | 89.89 | 11.47 | 12.80 | 67.07 | 70.32 | 91.08 | 10.23 | 152.20 | 11.49 | 138.62 | 40.08 |
| N.S.W. | S.D. | 0.80 | 0.74 | 0.72 | 5.51 | 1.00 | 1.49 | 0.92 | 11.70 | 0.78 | 10.86 | 2.77 |
| Tumut Creek | Mean | 89.56 | 11.96 | 14.36 | 62.59 | 68.65 | 91.10 | 8.66 | 164.36 | 10.23 | 153.72 | 44.68 |
| N.S.W. | S.D. | 0.82 | 0.97 | 0.65 | 3.57 | 1.21 | 1.95 | 0.78 | 13.47 | 0.57 | 6.50 | 2.08 |
| Kinglake | Mean | 88.06 | 12.49 | 15.23 | 62.58 | 68.41 | 90.87 | 9.96 | 161.29 | 11.22 | 154.94 | 45.25 |
| Vic. | S.D. | 0.49 | 0.62 | 0.53 | 3.39 | 1.94 | 1.31 | 0.63 | 13.55 | 0.47 | 8.34 | 6.33 |
| Fifth Creek | Mean | 88.85 | 13.32 | 13.07 | 72.30 | 70.75 | 90.65 | 10.55 | 163.46 | 10.86 | 153.62 | 40.07 |
| S.A. | S.D. | 0.48 | 0.65 | 0.60 | 4.26 | 1.33 | 1.49 | 1.32 | 8.70 | 0.76 | 7.19 | 4.00 |
| Glen Stuart | Mean | 88.35 | 11.84 | 13.47 | 67.59 | 71.73 | 92.32 | 9.70 | 162.82 | 10.54 | 155.65 | 42.13 |
| S.A. | S.D. | 1.18 | 1.04 | 0.97 | 7.00 | 1.56 | 1.47 | 0.60 | 10.68 | 0.71 | 12.34 | 3.29 |
| Seymour Creek | Mean | 89.36 | 11.24 | 14.42 | 58.00 | 70.28 | 92.35 | 9.47 | 158.64 | 11.03 | 152.76 | 40.02 |
| Vic. | S.D. | 2.00 | 0.52 | 0.75 | 3.87 | 0.81 | 1.60 | 0.56 | 10.26 | 0.34 | 7.45 | 3.48 |
| All Data | Min. | 85.6 | 9.9 | 11.5 | 51.6 | 66.7 | 87.2 | 7.4 | 123.1 | 8.4 | 121.4 | 30.6 |
| | Mean | 89.09 | 12.16 | 13.94 | 63.66 | 70.07 | 91.89 | 9.90 | 158.88 | 10.91 | 150.94 | 41.93 |
| | Max. | 95.0 | 15.0 | 16.4 | 80.0 | 73.6 | 95.3 | 12.2 | 184.0 | 13.3 | 176.0 | 53.0 |

| Pel/ Pel. An. | Pre Pel./ S.L. | Pec.Pel./ S.L. | Pel.An./ S.L. | H.L./S.L. | H.W./H.L. | H.D./H.L. | Sn.L./ H.L. | P.O.H.L./ H.L. | I.O.W./H.L. | E.D./H.L. | L.U.J./H.L. | L.L.J./H.L. | W.G./H.L. | N |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 53.54 | 52.11 | 30.04 | 23.51 | 22.97 | 65.02 | 56.59 | 33.14 | 54.71 | 42.63 | 19.98 | 39.90 | 36.43 | 41.77 | |
| 2.52 | 0.87 | 1.26 | 0.91 | 0.50 | 2.74 | 2.54 | 1.68 | 2.66 | 3.00 | 1.47 | 1.06 | 1.92 | 1.57 | 10 |
| 51.94 | 52.11 | 31.41 | 23.07 | 22.68 | 60.23 | 54.60 | 29.34 | 52.50 | 37.30 | 20.38 | 37.04 | 33.65 | 32.96 | |
| 3.55 | 3.18 | 1.20 | 0.87 | 0.47 | 3.28 | 2.33 | 1.43 | 2.40 | 1.38 | 1.29 | 1.47 | 1.48 | 2.35 | 10 |
| 49.17 | 55.28 | 32.34 | 23.33 | 23.37 | 60.61 | 53.67 | 30.60 | 53.58 | 38.21 | 21.44 | 42.49 | 40.71 | 38.63 | |
| 4.80 | 1.69 | 1.70 | 1.36 | 0.55 | 2.36 | 3.69 | 1.41 | 1.39 | 1.33 | 1.31 | 2.29 | 1.53 | 2.90 | 10 |
| 42.81 | 52.43 | 32.33 | 25.40 | 21.50 | 60.85 | 55.98 | 29.94 | 56.21 | 40.13 | 17.59 | 38.94 | 34.92 | 35.57 | |
| 3.51 | 1.47 | 1.44 | 0.95 | 1.17 | 2.55 | 3.40 | 2.57 | 3.74 | 1.33 | 1.52 | 2.47 | 1.39 | 2.32 | 10 |
| 42.44 | 54.23 | 33.74 | 25.70 | 21.34 | 60.18 | 54.93 | 28.67 | 56.47 | 38.31 | 18.10 | 36.23 | 31.66 | 37.56 | |
| 5.38 | 1.81 | 2.64 | 0.32 | 1.17 | 1.92 | 4.73 | 2.28 | 3.98 | 1.68 | 1.99 | 1.75 | 1.82 | 3.00 | 7 |
| 53.39 | 51.48 | 29.71 | 22.32 | 22.72 | 58.83 | 53.13 | 30.07 | 50.60 | 37.49 | 23.83 | 38.61 | 36.72 | 34.06 | |
| 6.41 | 1.52 | 1.36 | 1.78 | 0.92 | 3.98 | 4.07 | 3.01 | 3.38 | 2.28 | 1.89 | 1.49 | 1.50 | 2.95 | 10 |
| 43.00 | 53.92 | 33.08 | 24.05 | 22.64 | 67.86 | 59.74 | 31.13 | 53.80 | 40.93 | 17.92 | 38.85 | 35.12 | 42.84 | |
| 4.13 | 1.62 | 2.58 | 1.27 | 0.67 | 3.84 | 3.93 | 1.48 | 4.01 | 1.52 | 1.17 | 2.34 | 2.58 | 3.75 | 10 |
| 47.81 | 50.96 | 32.14 | 23.91 | 20.49 | 61.07 | 56.46 | 31.31 | 53.65 | 40.79 | 19.15 | 37.73 | 34.71 | 36.15 | |
| 3.55 | 1.91 | 1.87 | 1.39 | 0.84 | 3.71 | 4.33 | 1.87 | 1.96 | 1.50 | 1.22 | 1.87 | 1.63 | 1.60 | 10 |
| 48.37 | 54.44 | 34.09 | 23.72 | 21.16 | 65.19 | 54.47 | 32.05 | 55.91 | 41.98 | 17.32 | 38.28 | 34.17 | 41.12 | |
| 3.47 | 0.97 | 1.23 | 1.25 | 0.76 | 2.49 | 2.58 | 1.62 | 1.50 | 3.21 | 1.63 | 2.41 | 1.94 | 1.43 | 10 |
| 50.87 | 50.77 | 30.81 | 23.62 | 21.66 | 68.47 | 55.66 | 33.31 | 56.39 | 40.11 | 17.43 | 38.80 | 34.41 | 40.81 | |
| 5.18 | 1.22 | 1.25 | 0.52 | 0.94 | 2.51 | 2.29 | 1.45 | 2.07 | 1.53 | 1.40 | 2.53 | 2.50 | 2.23 | 10 |
| 54.27 | 51.92 | 30.66 | 23.63 | 24.13 | 64.88 | 53.47 | 31.35 | 53.13 | 40.84 | 17.88 | 41.40 | 38.29 | 39.82 | |
| 4.21 | 1.03 | 2.29 | 1.09 | 0.54 | 2.00 | 2.84 | 1.93 | 1.63 | 2.02 | 1.62 | 2.06 | 1.30 | 3.04 | 10 |
| 46.15 | 53.58 | 33.25 | 25.50 | 20.75 | 62.85 | 60.32 | 29.35 | 56.90 | 39.17 | 19.90 | 37.97 | 36.15 | 38.58 | |
| 2.30 | 0.97 | 1.09 | 1.17 | 0.61 | 2.27 | 2.22 | 0.77 | 1.76 | 0.80 | 0.92 | 0.37 | 1.10 | 2.78 | 6 |
| 47.91 | 53.76 | 31.62 | 23.98 | 22.86 | 58.82 | 50.99 | 29.81 | 55.34 | 37.72 | 20.46 | 38.28 | 36.03 | 36.93 | |
| 2.96 | 1.74 | 2.03 | 0.97 | 0.86 | 2.90 | 1.85 | 2.79 | 2.54 | 1.93 | 1.13 | 1.98 | 2.31 | 2.29 | 15 |
| 46.93 | 52.58 | 32.12 | 23.93 | 22.34 | 63.58 | 55.48 | 31.58 | 54.04 | 40.25 | 18.39 | 39.62 | 35.47 | 42.00 | |
| 4.99 | 1.04 | 0.81 | 1.18 | 0.99 | 3.23 | 3.23 | 2.05 | 3.03 | 2.13 | 1.65 | 3.50 | 1.95 | 1.96 | 10 |
| 35.2 | 46.2 | 27.8 | 19.8 | 18.6 | 54.1 | 47.5 | 23.1 | 44.0 | 33.3 | 15.2 | 33.3 | 28.6 | 29.2 | |
| 48.47 | 52.83 | 31.95 | 23.98 | 22.19 | 62.74 | 55.39 | 30.83 | 54.52 | 39.70 | 19.27 | 38.87 | 35.67 | 38.48 | |
| 66.7 | 57.7 | 37.6 | 26.8 | 25.1 | 73.2 | 69.1 | 37.5 | 61.5 | 45.8 | 27.5 | 45.7 | 42.9 | 47.6 | 138 |

Colour pattern is, to some extent, associated with features of the environment. Contrasting blotched or spotted patterns simulate the shadow patterns in small, clear exposed streams with gravel or stony beds, such as often occur above the snowline. On the Dargo High Plains, however, the fish occur in still, shallow pools with a dark, almost black substrate, and such fish are very dark in colour with little or no colour pattern. Light coloured fishes with little or no pattern are typical of streams with paler coloured substrates, even though deeply shaded, and also of streams that are relatively deep or turbid. Where there is deep shade and a dark substrate, relatively broad markings occur and the general ground colour is dark.

There are no distinctive colour pattern changes associated with stages of development, such as occur in *G. truttaceus* and *G. brevipinnis,* although the colour pattern does tend to become more fragmented with growth.

SIZE: *G. olidus* is amongst the "typical" moderate-sized galaxiids, reaching a known maximum length of 135 mm L.C.F. The size attained varies widely from population to population; in some the fish appear to reach no more than 60-70 mm, in others fish exceeding 80-90 mm are not uncommon.

HABITAT: *G. olidus* occurs most commonly in flowing waters and is typically taken in small, gravelly or sand-bedded streams, from sea level to about 1800 m altitude (near the summit of Mt Kosciusko). It is also found in small mountain tarns. It is sometimes cryptic but may live openly in shallow pools in loose shoals. Although McCulloch (1915) claimed that the fish at high altitude on Mt Kosciusko descend to lower elevations during the winter, they have been observed at an altitude of about 1700 m on the Bogong High Plains, in small tarns surrounded by thick snow.

LIFE HISTORY: The whole life cycle of *G. olidus* is completed in fresh water. A marine whitebait stage is not known, and fish from Pretty Valley, Bogong High Plains, suffered dehydration and failed to acclimate to sea water diluted to one-third of normal salinity. Spawning commonly occurs in the spring months (September to November), but in alpine populations, at least, it may extend to April. No significant spawning migration is known. Aspects of the life history of *G. olidus* were examined by Walford (1928, 1940, 1941) — identified as *G. coxii* (syn. *G. brevipinnis*). Walford studied populations in both natural conditions (near Katoomba, Blue Mountains, New South Wales) and in a garden pond, and he found that two main hatches of fry occurred each year — in September and November, except that the September hatch was missed if the spring was unusually cold. The garden pond population bred regularly over a period of 13 years. Newly hatched larvae grew from 5 mm to about 25 mm in six weeks, and to 32 mm in eight weeks. The maximum size recorded was 127 mm. Individual specimens were reportedly kept for 15 years, and an estimated age of 19 years was given for one of Walford's specimens by Whitley (1964). These ages seem unlikely considering known growth rates and longevity in other galaxiid species (Cadwallader, 1977; Eldon, 1978; Hopkins, 1971).

In Pretty Valley (and the neighbouring Rocky Valley), on the Bogong High Plains in Victoria, galaxiids and introduced brown trout (*Salmo trutta*) display an essentially complementary distribution; overlapping ranges were recorded on only one occasion. Trout occupy the main body of the stream, while galaxiids are usually found only in situations apparently inaccessible to trout, such as above waterfalls, or in small tarns adjacent to the main stream. Assuming that the galaxiids were once continuously distributed, trout appear to have fragmented the range of *G. olidus* into small, isolated populations.

Tilzey (1974) presented a preliminary report on the effects of rainbow trout *(Salmo gairdnerii* on *G. olidus* (misidentified as *G. coxii*), noting that where both trout and *G.*

*olidus* "occurred together, the galaxiids were extremely scarce. . . . Sampling of one feeder stream in 1971 and 1974 spanned the invasion by rainbow trout of water previously occupied by *Galaxias coxii (sic)* and showed the latter species to be completely exterminated, although the biomass of *G. olidus* above a natural waterfall barrier remained unaltered". Tilzey (1976) has since more fully documented this event, demonstrating quite clearly that invasion of a stream by trout has led to the extermination of *G. olidus* which is shown, like other galaxiids (McDowall, 1968d) to be susceptible to decline in the face of competition from trout. Fletcher (1978) has presented similar observations.

DISTRIBUTION: *G. olidus* is generally distributed in upland and sub-alpine areas of southeastern Australia from southern Queensland to eastern South Australia, in systems draining to the coast from the Great Dividing Range as well as those draining into the inland Murray-Darling drainage (Fig. 9). It is not known from coastal drainages in northern New South Wales between the Macleay and Hawkesbury Rivers; this may represent either a gap in knowledge or a real distributional gap — existing data do not suffice to determine which. Nor is the species known from the low elevation, flat, and dry area between the Grampian Mountains at the western end of the Great Dividing Range and the hills of the Flinders Range as they extend south into the Fleuriau Peninsula. One specimen has been identified from Kangaroo Island (South Australia — SAM No. F.1115 collected in 1883) but further confirmation of the occurrence of *G. olidus* on the island is desirable.

Altitudinal range is extensive, the species being recorded from near sea level to an altitude of 1800 m.

### **Galaxias johnstoni** Scott

Fig. 10, 12

*Galaxias (Galaxias) johnstoni* Scott, 1936: 91 (holotype: QVML HT.948, (type no. 70) seen; paratypes: (2) QVML type no. 71, seen; (1) BMNH 1966.5.6.: 3, not seen; Scott (1936) stated that he intended to send paratypes to AMS and AIAC; it appears that neither institution received type material; type locality: Brown's Marsh Rivulet, Clarence River, Tasmania); 1941: 60; 1942: 54.

*Galaxias johnstoni* — Whitley, 1956a: 34; 1956b: 39; Munro, 1957b: 17; Whitley, 1964: 35; Frankenberg, 1966a: 164; 1966b: 23; 1967: 227; 1968: 270; Scott, 1968: 8; Andrews, 1973: 105; Frankenberg, 1974: 121; Andrews, 1976: 317; Lake, 1978: 22.

TAXONOMY: As Andrews (1976) notes, the listing by Munro of the Nive River as the type locality is incorrect.

Material of *G. johnstoni* has been very meagre in the past. Frankenberg (1974) reported that only seven specimens were then known, to which Andrews (1976) added two while noting that three of Frankenberg's (1974) fish could not be located. Additional material was obtained by Mr W. Fulton, Tasmanian Inland Fisheries Commission, from Clarence Lagoon, near the mouth of the Clarence River, enabling the status of *G. johnstoni* to be assessed more adequately. Description here is based on 20 newly examined specimens as well as data on the types.

*G. johnstoni* is similar and obviously closely related to another Tasmanian galaxiid — *G. pedderensis* Frankenberg. Frankenberg (1967) noted that "The lower number of vertebrae (given as 49-52 in *G. pedderensis* and 54 in *G. johnstoni*), the single pyloric caecum (cf. 2 in *G. johnstoni*), the narrower caudal peduncle (32.5-37.0, mean = 34.6% of

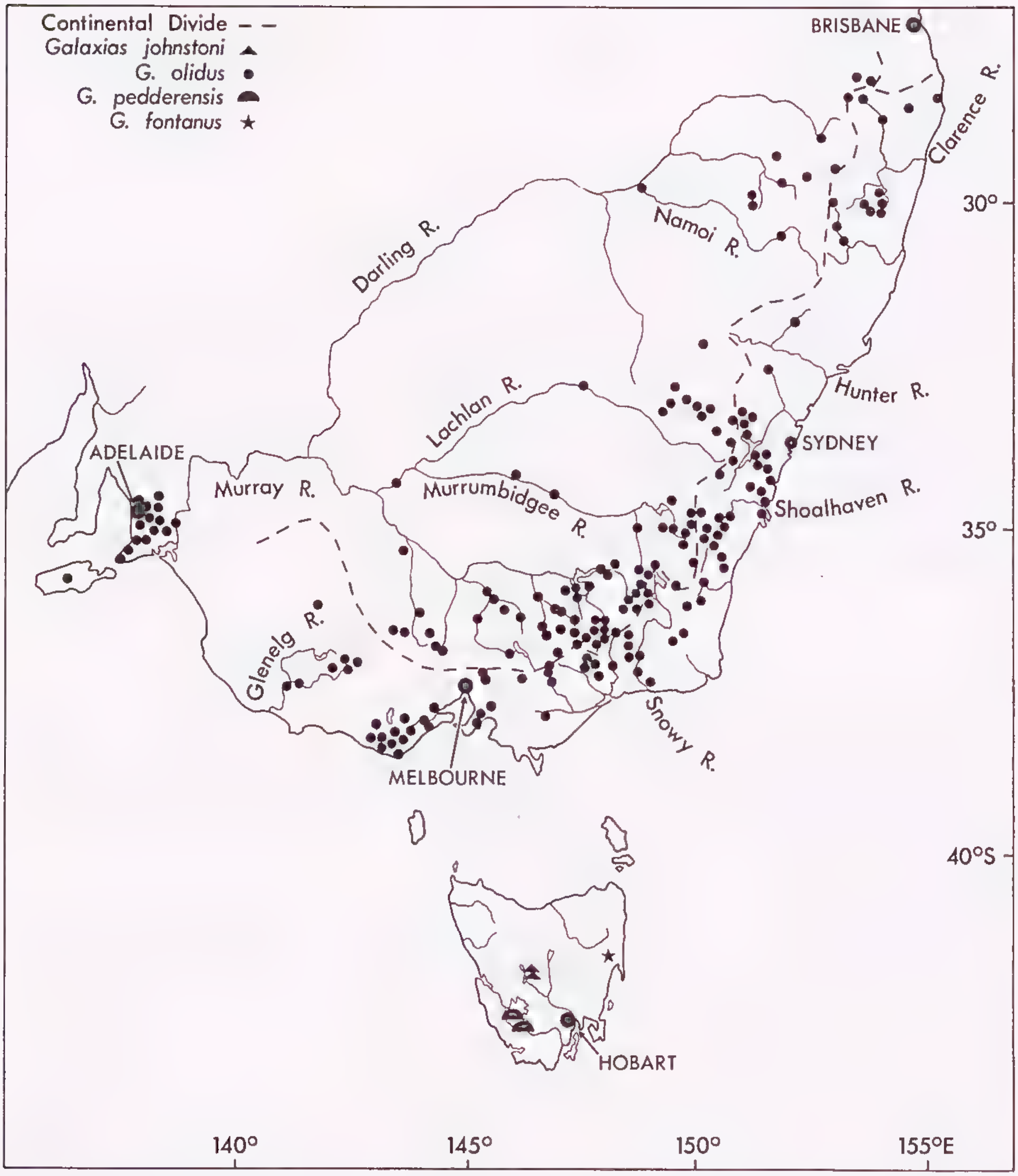

Fig. 9. Distribution of *Galaxias olidus, G. johnstoni, G. pedderensis* and *G. fontanus.* One symbol may represent more than one locality.

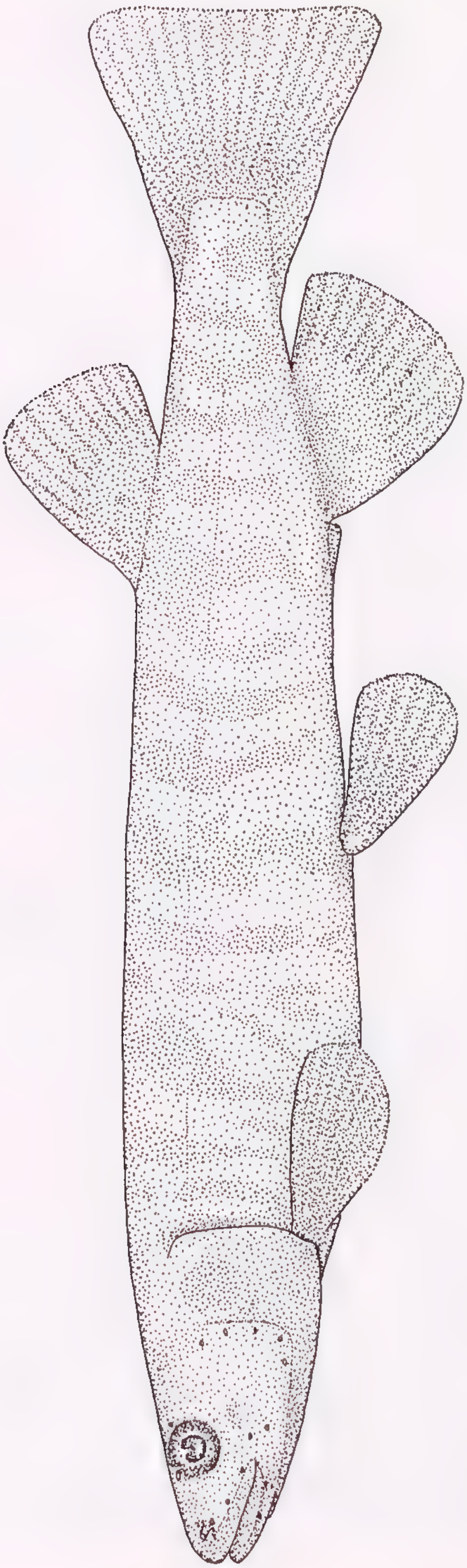

Fig. 10. *Galaxias johnstoni* Scott; Clarence Lagoon, Tas., 86.5 mm L.C.F.

the dorsal length, cf. 39.0-47.0, mean = 43.1%) and the larger head (23.1-26.0, mean = 24.0% of S.L. cf. 21.0- 23.0, mean = 22.0%) serve to distinguish *G. pedderensis* from *G. johnstoni*". Frankenberg's data were based on small examples of both species (40.5-60.0 mm S.L. in *G. johnstoni* and 32.0-51.5 mm S.L. in *G. pedderensis)* and on only three examples of *G. johnstoni.* Andrews (1976: 317) distinguished the two species as follows: *G. johnstoni* "differs from *G. pedderensis* in having a slightly smaller head, smaller ventral fins, and a shorter ventral-anal interspace".

Differences between *G. johnstoni* and *G. pedderensis* are slight. The difference in vertebral count noted by Frankenberg (1967) is shown to be much less when additional material is incorporated (51-54 in *G. johnstoni,* 49-52 in *G. pedderensis* – Table 6). Differences of this degree are common between discrete, conspecific populations of many galaxiid species (see McDowall, 1970a, 1971, 1972a). No differences of any taxanomic significance are evident in fin ray counts (Table 6). Frankenberg (1967) reported only one pyloric caecum in *G. pedderensis* but two in *G. johnstoni.* Andrews (1976:320) however, reported "Pyloric caeca variable, 0, 1 or 2" in *G. pedderensis* but did not mention their occurrence in *G. johnstoni.* Our observations show that *G. johnstoni* usually has two, occasionally three moderately long caeca while *G. pedderensis* may have none, one or two as Andrews has indicated.

In body proportions *G. johnstoni* is generally considerably stouter in build (Table 7), having a deeper caudal peduncle and broader and deeper head; the predorsal distance is somewhat greater in *G. johnstoni* and the pectoral fins are shorter.

Colouration differs. *G. johnstoni* has bold and contrasting dark bars or vermiculations dorsolaterally and laterally, these tending to coalesce on the back, making the back dark in colour. *G. pedderensis* tends, rather to have discrete, well separated darker brownish blotches on the back and passing over on to the upper sides, but below the lateral line these abruptly fragment to form a fine reticulum, or vermiculations, that extend latero-ventrally but fail on the belly. *G. johnstoni* has a few small spots on the bases of the unpaired fins but in *G. pedderensis* these are much more numerous and extend well out onto the fins. All the individual and quantifiable differences between these two species are small, but they combine to give *G. johnstoni* a very different appearance from *G. pedderensis.* The two species are therefore retained as distinct.

DIAGNOSIS: Characterised by tubular trunk, bluntish snout, large mouth, the gape reaching back well below the eye, and the anal origin below the middle to rear of dorsal fin.

Differs from *G. brevipinnis* and *G. olidus* in characters discussed in the diagnoses of these two species (pp.462 and 479 respectively); differs from *G. pedderensis* in regularly having two pyloric caeca of moderate length (often 0-1, sometimes 2 in *G. pedderensis*), in being stouter in build, and in having the lateral pigmentation not fragmented below the lateral line, as it frequently is in *G. pederensis; G. johnstoni* tends to be more darkly pigmented than *G. pedderensis.* The differences are generally small. Differs from *G. fontanus* in having four pores in row below eyes, and having two pyloric caeca.

DESCRIPTION: A moderate-sized species, the trunk tubular, the back and belly little arched, body deepest in front of pelvic fins at about mid-abdomen, tapering to a moderately slender caudal peduncle, which is much longer than deep. Head of moderate length, somewhat depressed, broader than deep. Snout tapering and bluntly pointed; mouth large, slightly oblique, reaching back as far as middle of eye; jaws equal. Eyes small, set a little below upper head profile, interorbital broad and slightly convex. Jaws with slight enlargement of lateral canines; mesopterygoidal and lingual teeth strong. Gill rakers short and stout (Fig. 43). Two pyloric caeca of moderate length (Fig. 45). Laterosensory pores as in Fig. 47.

Fins small, thick and fleshy at bases. Dorsal and anal fins short-based, high and rounded, posterior rays long, the fins extending well back beyond fin bases. Anal fin origin below or behind mid-point of dorsal fin base. Pectoral fins small to moderate, oval-shaped, insertion low lateroventrally, fin lamina more or less horizontal. Pelvic fins of moderate size, inserted somewhat behind mid-point of standard length. Caudal fin slightly forked to truncated, fin tips rounded, fin depth a little less than body depth, caudal peduncle flanges well-developed.

Variation: meristic: see Table 6
morphometric: see Table 7

COLOUR: Colour when alive, described by Andrews (1976: 317) as "dark greenish-black on the back and sides, light silvery fawn below, back and sides of head and body marked with irregular brownish-black patches, ventral surface unmarked. A sharp line of demarcation running below and parallel to the lateral line separates the marked dorsal surface from the unmarked ventral surface. In live specimens numerous spots of bright metallic gold are visible over the entire body, with a conspicuous patch on the operculum. . . . all the fins clear. . . ."

In preservative grey-olive with boldly contrasting broad, dark brown vermiculations to bands across the back and sides, extending forwards also on to the head. Bases of unpaired fins somewhat spotted. Belly creamish-grey.

SIZE: *G. johnstoni* is known to reach a length of 98 mm L.C.F. Specimens over 70 mm are well represented amongst the few known specimens.

HABITAT: Little is known about the habitat of *G. johnstoni;* it has been taken both in a lacustrine habitat in Clarence Lagoon, and in flowing waters both entering and draining the lagoon. Too few specimens have been collected to properly characterise the habitat.

LIFE HISTORY: The life history is unstudied. There is no evidence to suggest a marine phase, or any migration of significance.

DISTRIBUTION: *G. johnstoni* is known only from Clarence Lagoon, its tributaries, and the upper reaches of the Clarence River, which drains Clarence Lagoon, and which is a tributary of the Nive River, a part of the Derwent River system, Tasmania (Fig. 9).

### **Galaxias pedderensis** Frankenberg

Fig. 11, 12

*Galaxias pedderensis* Frankenberg, 1967: 268 (holotype: TMH D.941, seen; paratypes: (9) NMVM 379-387, seen; type locality: Lake Pedder, southern Tasmania, near the mouth of the inflowing stream from Lake Maria — the type locality has since been obliterated by the flooding of Lake Pedder and its environs to form a water storage lake); Andrews, 1971: 1; Lake, 1971: 20; Bayly et al., 1972: 46; Dixon, 1972: 121; Lynch, 1972: 14; Johnston, 1972: 43; Andrews, 1973: 106; Lake, 1974: 449; Frankenberg, 1974: 123; Andrews, 1976: 319; Lynch, 1977: 14; Lake, 1978: 22.

TAXONOMY: The similarity between, and problems in the separation of *G. pedderensis* and *G. johnstoni* are discussed in the taxonomy section of *G. johnstoni* (p.489), to which the reader is referred.

Table 6. Meristic variation in *Galaxias johnstoni, G. pedderensis* and *G. fontanus.*

| | | *G. johnstoni* | *G. pedderensis* | *G. fontanus* |
|---|---|---|---|---|
| Dorsal rays — segmented | 7 | | | 4 |
| | 8 | 4 | 4 | 11 |
| | 9 | 12 | 19 | 5 |
| | 10 | 4 | 13 | |
| | 11 | | 1 | |
| total | 9 | | | 7 |
| | 10 | 5 | 3 | 8 |
| | 11 | 9 | 14 | 5 |
| | 12 | 5 | 14 | |
| | 13 | 1 | 6 | |
| Anal rays — segmented | 9 | 3 | 3 | 4 |
| | 10 | 11 | 6 | 11 |
| | 11 | 6 | 24 | 5 |
| | 12 | | 3 | |
| | 13 | | 1 | |
| total | 11 | 3 | | 1 |
| | 12 | 5 | 5 | 8 |
| | 13 | 8 | 20 | 10 |
| | 14 | 4 | 9 | 1 |
| | 15 | | 2 | |
| | 16 | | 1 | |
| Pectoral rays | 10 | | | 12 |
| | 11 | 1 | 2 | 8 |
| | 12 | 7 | 20 | |
| | 13 | 12 | 10 | |
| | 14 | | 5 | |
| Vertebrae | 49 | 1 | | |
| | 50 | 7 | | 1 |
| | 51 | 9 | 9 | 9 |
| | 52 | 1 | 4 | 8 |
| | 53 | | 6 | 2 |
| | 54 | | 2 | |
| Gill rakers | 9 | 1 | | |
| | 10 | 1 | 2 | |
| | 11 | 3 | 13 | 2 |
| | 12 | 5 | 7 | 7 |
| | 13 | 6 | 4 | 9 |
| | 14 | 3 | 3 | 2 |
| | 15 | 1 | 6 | |
| | 16 | | 1 | |
| | 17 | | 1 | |

*Table 7. Morphometric variation in Galaxias johnstoni, G. pedderensis and G. fontanus. Figures are given as percentages of denominators in ratios.*

| | *G. johnstoni* | | | | *G. pedderensis* | | | | *G. fontanus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Min. | Mean | Max. | S.D | Min. | Mean | Max. | S.D. | Min. | Mean | Max. | S.D. |
| S.L./T.L. | 85.6 | 87.96 | 89.3 | 1.08 | 86.4 | 87.94 | 89.8 | 0.91 | 85.3 | 86.76 | 88.4 | 0.89 |
| B.D.V./S.L. | 11.0 | 12.03 | 13.1 | 0.59 | 8.7 | 11.82 | 14.8 | 1.60 | 13.1 | 14.36 | 16.3 | 0.92 |
| L.C.P./S.L. | 11.4 | 14.16 | 16.5 | 1.14 | 13.4 | 15.51 | 17.2 | 0.96 | 14.7 | 16.40 | 17.9 | 0.96 |
| D.C.P./L.C.P. | 57.7 | 64.74 | 75.9 | 5.06 | 44.7 | 59.04 | 64.6 | 9.89 | 59.4 | 65.02 | 73.0 | 4.15 |
| PreD./S.L. | 67.0 | 70.37 | 74.5 | 2.05 | 65.7 | 68.29 | 71.1 | 2.08 | 68.8 | 71.24 | 73.4 | 1.15 |
| PreD./PreA. | 89.5 | 92.85 | 96.7 | 1.65 | 90.9 | 93.76 | 96.7 | 1.48 | 94.8 | 97.91 | 100.0 | 1.38 |
| L.D.B./S.L. | 8.0 | 9.34 | 10.8 | 0.64 | 7.3 | 9.91 | 12.8 | 1.37 | 9.2 | 10.06 | 11.8 | 0.59 |
| M.L.D./L.D.B. | 154.5 | 172.69 | 193.3 | 9.14 | 135.7 | 161.11 | 191.7 | 12.51 | 159.1 | 176.87 | 192.6 | 8.54 |
| L.A.B./S.L. | 10.0 | 10.91 | 12.7 | 0.72 | 10.4 | 12.35 | 14.3 | 1.06 | 12.0 | 13.66 | 15.3 | 0.92 |
| M.L.A./L.A.B. | 142.9 | 153.38 | 172.2 | 8.61 | 120.0 | 144.18 | 166.7 | 9.37 | 137.0 | 146.99 | 154.5 | 6.18 |
| Pec./Pec.Pel. | 44.7 | 52.67 | 63.2 | 4.74 | 40.7 | 50.90 | 74.3 | 6.78 | 48.0 | 55.11 | 65.7 | 4.39 |
| Pel./Pel.An | 55.1 | 61.48 | 70.3 | 4.82 | 56.8 | 66.32 | 79.2 | 5.47 | 57.9 | 65.63 | 71.8 | 3.85 |
| PrePel/S.L. | 49.0 | 54.01 | 57.3 | 1.79 | 51.0 | 53.82 | 58.9 | 2.09 | 49.2 | 51.50 | 53.7 | 1.29 |
| Pec.Pel./S.L. | 27.0 | 30.98 | 32.7 | 1.45 | 27.2 | 30.47 | 34.1 | 1.59 | 27.2 | 29.47 | 31.1 | 1.08 |
| Pel.An./S.L. | 20.0 | 22.75 | 24.5 | 1.09 | 18.40 | 20.44 | 21.9 | 1.21 | 19.9 | 21.84 | 23.8 | 0.95 |
| H.L./S.L. | 23.0 | 25.09 | 27.1 | 1.15 | 21.4 | 24.93 | 26.8 | 0.96 | 23.4 | 24.65 | 25.8 | 0.68 |
| H.W./H.L. | 55.8 | 62.21 | 69.2 | 3.90 | 43.5 | 55.08 | 65.3 | 5.64 | 59.6 | 62.57 | 66.7 | 1.95 |
| H.D./H.L. | 52.6 | 55.91 | 61.3 | 2.20 | 43.5 | 50.83 | 59.7 | 3.53 | 48.9 | 52.99 | 57.7 | 2.18 |
| Sn.L./H.L. | 28.1 | 32.28 | 37.5 | 2.27 | 26.1 | 30.75 | 34.9 | 1.92 | 31.7 | 34.03 | 37.8 | 1.64 |
| P.O.H.L./H.L. | 48.9 | 52.82 | 56.5 | 2.05 | 45.9 | 51.61 | 59.4 | 2.40 | 44.7 | 50.95 | 55.0 | 2.48 |
| I.O.W./H.L. | 34.1 | 37.75 | 42.5 | 2.32 | 26.7 | 33.94 | 38.9 | 3.29 | 38.3 | 41.93 | 44.9 | 2.03 |
| D.E./H.L. | 17.1 | 20.85 | 25.6 | 2.55 | 15.7 | 20.90 | 28.8 | 2.34 | 20.3 | 22.89 | 25.5 | 1.40 |
| L.U.J./H.L. | 37.2 | 42.21 | 46.8 | 2.40 | 35.6 | 41.23 | 47.6 | 3.18 | 42.5 | 45.20 | 47.4 | 1.65 |
| L.L.J./H.L. | 34.9 | 39.30 | 44.1 | 2.36 | 32.5 | 38.44 | 44.4 | 2.72 | 39.7 | 43.46 | 45.6 | 1.45 |
| W.G./H.L. | 34.9 | 38.38 | 43.2 | 2.71 | 22.5 | 34.51 | 47.2 | 5.95 | 34.0 | 38.57 | 43.6 | 2.44 |
| N | | 20 | | | | 37 | | | | 20 | | |

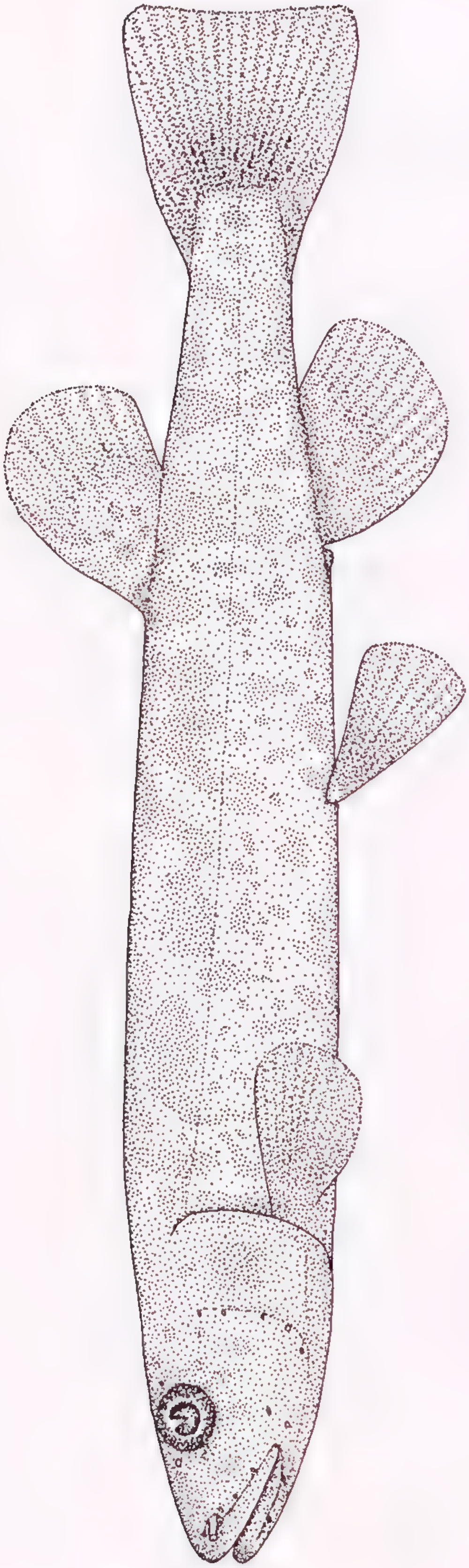

Fig. 11. *Galaxias pedderensis* Frankenberg; Lake Pedder, Tas., 87 mm L.C.F.

*G. pedderensis* is known only from Lake Pedder and its environs, and no examination of variation between populations was undertaken.

DIAGNOSIS: Characterised by very elongate, slender form and large strongly depressed head, the eye more or less at the dorsal head profile and the interorbital flat. The anal fin is well back from the dorsal fin origin.

Differs from *G. brevipinnis, G. olidus* and *G. johnstoni* in characters discussed in the diagnoses of these three species (pp.462, 479 and 492 respectively). Differs from *G. fontanus* in having only four pores in row below eyes, in having only slight enlargement of canine teeth in jaws, and usually fewer pectoral fin rays.

DESCRIPTION: A moderate-sized and very slender species, the trunk rounded in section or slightly compressed, the dorsal and ventral trunk profiles about parallel, little arched, greatest body depth behind head; strongly depressed anteriorly on head, becoming increasingly compressed behind vent. Caudal peduncle long and slender, much longer than deep. Head moderately long, dorsally flattened, much broader than deep, snout long and flattened, tapering to a slender, rounded point. Mouth slightly oblique, large, extending back well below eye, jaws about equal. Eyes small, set at about upper head profile, interorbital broad and flat. Jaws with slightly enlarged lateral canine teeth; mesopterygoidal and lingual teeth strong. Gill rakers very short (Fig. 43) and stout; 0-2 pyloric caeca of moderate length (Fig. 45). Disposition of laterosensory pores as in Fig. 47.

Fins mostly small, somewhat thickened and fleshy at bases. Dorsal and anal fins short-based, but high and rounded, posterior rays long, the fins extending back well behind fin bases; anal origin set well behind dorsal origin, often below middle of dorsal base or further back. Pectoral fins small and rounded, inserted low lateroventrally with lamina of fin tending to face downwards. Pelvic fin insertion somewhat behind mid-point of standard length. Caudal fin emarginate to truncate, fin tips rounded, fin depth about equal to body depth, peduncle flanges moderately developed.

Variation: meristics: see Table 6.
morphometric: see Table 7.

COLOUR: Colour when alive variable, often extremely bold and contrasting brown and off-white bands on the back and sides, the pattern very irregular and extending forwards on to the head. The darker areas on the back and trunk are about as large as the paler areas. Belly a pale off-white. Dark pattern extends onto fleshy fin bases.

Colour in preservative boldly contrasting and very irregular grey-brown and creamish-white vermiculations, coarse above lateral line but becoming suddenly fragmented at lateral line and much finer below it; fin bases spotted, belly unmarked.

SIZE: *G. pedderensis* grows to a maximum known length of 110.5 mm L.C.F. and commonly reaches a length exceeding 70 mm.

HABITAT: *G. pedderensis* was taken from amongst rocks and boulders, less often from amongst submerged vegetation around the shores of Lake Pedder. It is also found amongst cover in streams flowing into Lake Pedder. The water of Lake Pedder is deeply stained brown and is likely to have low pH.

Frankenberg (1967) reported the species from Lake Pedder, prior to its inundation following construction of a large dam across the outlet river which resulted in raised water levels. Frankenberg found that the fish were abundant near the edge of the lake and in a stream flowing into it. Some fish were also found with *G. parvus* in a small pond near the shores of Lake Pedder. *G. pedderensis* remains abundant in the new enlarged lake.

LIFE HISTORY: No data are available on the life history of *G. pedderensis,* although Andrews (1976:321) speculated that spawning "would appear to take place during the late autumn or winter, presumably in the upper reaches of streams flowing into Lake Pedder and the upper Serpentine River. Mature females were taken from a pool below a man-made waterfall some 120 cm in height and their accumulation there may indicate an upstream migration".

DISTRIBUTION: *G. pedderensis* is known only from Lake Pedder and waters draining into the lake (Fig. 9).

### **Galaxias fontanus** Fulton

Fig. 12, 13

*Galaxias fontanus* Fulton, 1978b: 2 (holotype: TMH D.1317, seen; paratypes: (4) TMH D. 1318-1321, seen; (4) QVML 1978/5/72 (type 254), seen; (4) AMS I.20157-001, seen; type locality: Swan River, eastern Tasmania, where State forestry MG road crosses this river).

DIAGNOSIS: An elongate, tubular, blunt-headed species with enlarged lateral canine teeth in the jaws, usually 5-6 open laterosensory pores in the series from beneath eyes to anterior nostril, and no pyloric caeca.

Differs from *G. brevipinnis, G. johnstoni* and *G. pedderensis* in characters listed in the diagnoses of these three species (pp.462, 492 and 497 respectively).

DESCRIPTION: A moderate-sized species, the trunk tubular, back and belly little arched, body deepest in front of pelvic fins, tapering to a moderately slender caudal peduncle which is longer than deep. Head of moderate length, depressed, much broader than deep. Snout bluntly pointed, mouth large, slightly oblique, reaching to about below middle of eyes; jaws about equal. Eyes small to moderate-sized, set at about upper head profile, interorbital broad and flat. Jaws with strong lateral canines; mesopterygoidal and lingual teeth strong; gill rakers very short and stout (Fig. 43); no pyloric caeca (Fig. 45); laterosensory pores as in Fig. 47, series from below eyes to anterior nostril usually with 5, sometimes 6, rarely 4 pores.

Fins small, thick and fleshy at bases. Dorsal and anal fins short-based, high and rounded, posterior rays long, the fins extending well back behind bases, anal origin below or a little behind dorsal origin. Pectoral fins short, oval-shaped, insertion low lateroventrally, fin lamina more or less horizontal. Pelvic fins of moderate size, inserted at about mid-point of standard length. Caudal fin slightly forked to emarginate, fin tips rounded, fin depth about equal to body depth, caudal peduncle flanges well developed.

Variation: meristic: see Table 6
morphometric: see Table 7

COLOUR: Colour when alive a dull greenish-olive with quite fine and irregular brownish markings, the belly a silvery-olive.

In preservative, brownish, the sides and back covered with dense and irregular vermiculations, fins without markings, dusky, the belly creamish-grey.

SIZE: *G. fontanus* is known to reach 96 mm L.C.F., and is not uncommonly 65 mm or more.

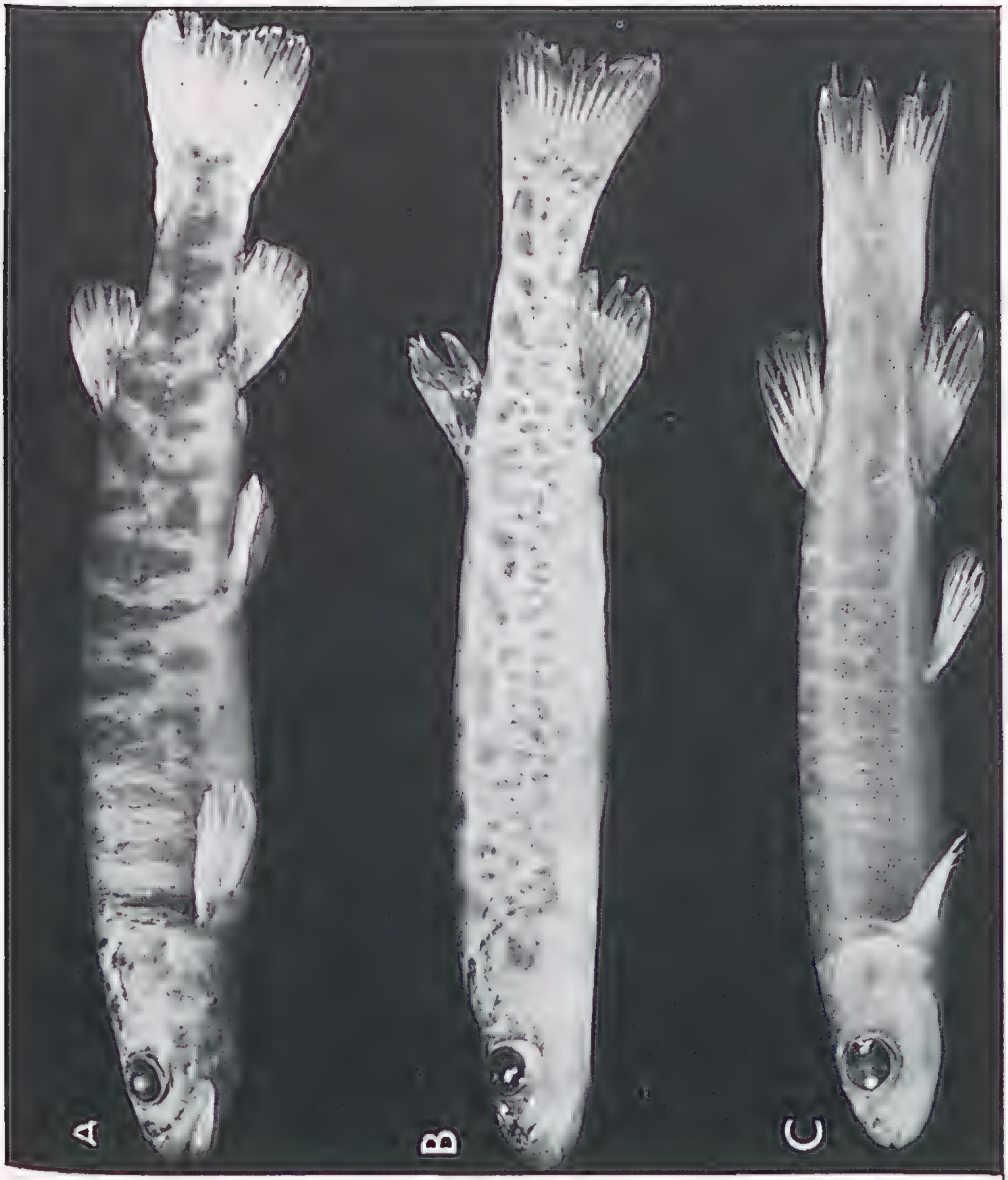

Fig. 12. Colour pattern in — **a.** *Galaxias johnstoni*, Clarence Lagoon, Tas. 89 mm L.C.F.; **b.** *G. pedderensis*, Lake Pedder, Tas., 64.5 mm; **c.** *G. fontanus*, Swan River, Tas., 64.5 mm L.C.F.

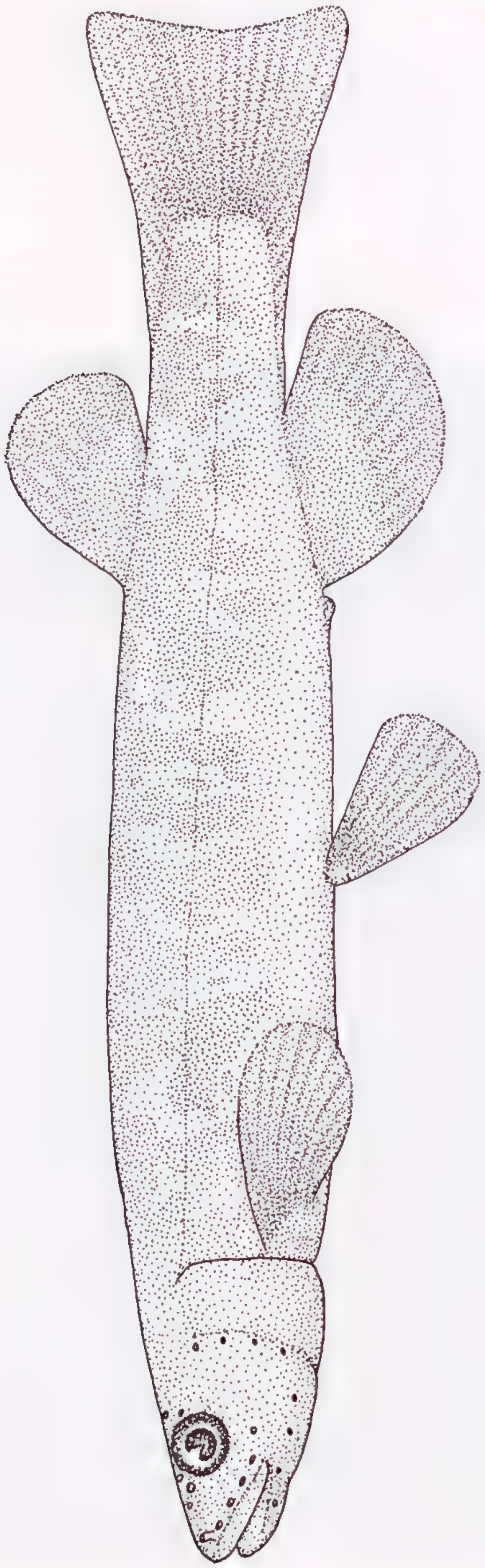

Fig. 13. *Galaxias fontanus*, Fulton; Swan River, Tas., 71 mm L.C.F.

HABITAT: The fish were collected free-swimming, or sheltering beneath rocks or marginal cover in gently to moderately swiftly flowing waters in a small, apparently spring-fed stream flowing through low, dry scrub. Numbers were much lower in the more swiftly flowing waters.

LIFE HISTORY: Juveniles 15-25 mm long were collected with the adults in January-February, indicating a spring-summer spawning and showing that the entire life cycle is completed in fresh water.

DISTRIBUTION: Known only from the upper reaches of the Swan River, eastern Tasmania (Fig. 9).

### **Galaxias truttaceus** Valenciennes

Fig. 14, 15

*Esox truttaceus* Cuvier, 1817: 390 (*nomen nudum*).

*Galaxias truttaceus* Valenciennes, in Cuvier and Valenciennes, 1846: 344 (syntypes (3) MNHN A.5311-3, not seen; type locality: Tasmania); Richardson, 1848: 75; Kner, 1865: 320; Günther, 1866: 209; Krefft, 1871: 84; Günther, 1880: 625; Klunzinger, 1880: 412; Macleay, 1881: 47; 1882: 209; Johnston, 1882: 130; Seal et al. 1883: lvi; Johnston, 1883: 130; 1891: 27; Ogilby, 1893: 177; 1896: 64 (*partim*); Regan, 1905: 378; Stead, 1906: 49; Fletcher, 1907: 567; Ogilby, 1908: 6; Johnston, 1909: iv; Anon, 1913: xvi; McCulloch, 1919: 49; Lord, 1923: 63; Lord and Scott, 1924: 33; Lord, 1927: 12; Walford, 1928: 274; Iredale and Whitley, 1932: 95; McCulloch, 1929: 48; Whitley, 1929: 46; Scott, 1934: 44; Whitley, 1935: 44; Mack, 1936: 99; Scott, 1936: 113; Blackburn, 1950: 160; Bertin and Esteve, 1950: 3; Whitley, 1956a: 30; 1956b: 39; 1957a: 7; 1957b: 8; 1964: 35; Lynch, 1965: 13; Scott, 1966: 244; Frankenberg, 1966a: 20; 1966b: 19; Lynch, 1966: 13; McDowall, 1967a: 842; 1968c: 177; Lynch, 1968: 9; Anon. 1968: 26; Scott, 1968: 1; McDowall, 1969: 804; Lynch, 1969: 23; 1970: 15; Whitley, 1970: 54; McDowall, 1970a: 420; 1970b: 18; 1971: 68; Scott, 1971a: 8; 1971b: 120; Lynch, 1971: 13; Dixon, 1972: 121; Andrews, 1973: 104; McDowall, 1973b: 97; Rosen, 1974: 317; McLean, 1974: 13; Scott, 1974: 254; Whitley, 1975: 64; Andrews, 1976: 305; Lynch, 1977: 13; Fulton, 1978a: 109; 1978b: 3; McDowall, 1978c: 209; McDowall and Fulton, 1978b: 663; Lake, 1978: 25; Backhouse and Vanner, 1978: 128.

*Galaxias forsteri* — Kner, 1867: 320 (*partim* — non *Galaxias forsteri* Valenciennes, in Cuvier and Valenciennes, 1846: 531, syn. *Galaxias argenteus* (Gmelin, 1789), New Zealand).

*Galaxias ocellatus* McCoy, 1867: 18 (holotype: unknown; type locality; Yarra River near Studley Park, Victoria); Castlenau, 1872: 175; Macleay, 1881: 47; 1882: 235; Lucas, 1890: 35; Ogilby, 1896: 68; Whitley, 1956a: 34.

*Galaxias truttaceous* — Anderson, 1900: 25; Butcher, 1946: 9; Lake, 1971: 20; Anon. 1974a: 13; 1974b: 12; (mispelling of *Galaxias truttaceus*).

*Galaxias (Galaxias) truttaceus* — Scott, 1936b: 89; 1938: 126; 1941: 55; 1942: 56.

*Galaxias (Galaxias) scopus* — Scott, 1936b: 95 (holotype: QVML HT. 949, seen; Scott indicated that he intended sending a paratype to the British Museum, but this fish was apparently never received by the museum and there is no paratype; type locality: small brackish stream, Clarke Island, Bass Strait); 1941: 60.

*Galaxias scopus* — Whitley, 1944: 264; 1956a: 34; 1956b: 39; 1957a: 7; 1957b: 34; 1964: 35; Stokell, 1966: 79; Scott, 1968: 8; Green, 1974: 2.

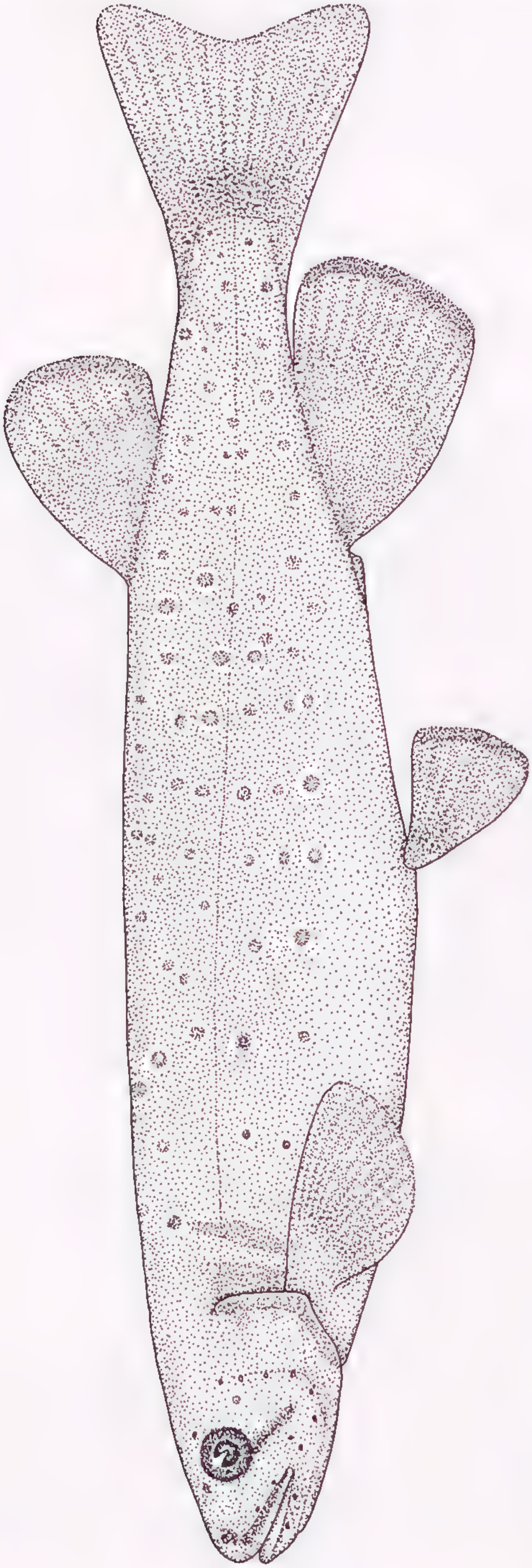

Fig. 14. *Galaxias truttaceus* Valenciennes, Triabunna, Tas., 135 mm L.C.F.

*Galaxias truttaceus hesperius* Whitley, 1944: 263 (holotype: WAM P. 2580 seen; paratypes: (2) AMS I.13280, seen; type locality: creek flowing into Taylors Inlet, Albany District, Western Australia); Whitley, 1947: 53; 1948: 11; 1956b: 39; 1957a: 7; Munro, 1957b: 16; Mees, 1961: 38; Gentilli, 1961: 488; Whitley, 1964: 35.

*Galaxias hesperius* — Whitley, 1956b: 34.

*Galaxias truttaceus scopus* — Munro, 1957b: 16; Gentilli, 1961: 488; Green, 1969: 27.

*Galaxias truttaceus truttaceus* — Munro, 1957b: 16; Gentilli, 1961: 488; Frankenberg, 1967: 226; Green and McGarvie, 1971: 30; Frankenberg, 1974: 123.

TAXONOMY: The name *truttaceus* was first used in the combination *Esox truttaceus* by Cuvier, (1817) as a footnote to his diagnosis of the genus *Galaxias*. It was based on material collected in Tasmania in the late 18th century. Because Cuvier published no description, the 1817 usage is a *nomen nudum*, and the name is attributable to Valenciennes, in Cuvier and Valenciennes (1846) where the species is described for the first time.

Stokell (1966: 78) claimed that "The name *truttaceus*, which is universally applied to the common black spotted species of Tasmania and Victoria, is of very doubtful validity. . . . The application of the name *truttaceus* to the Tasmanian fish appears to be a misidentification of a type species, and a new name or the reinstatement of a synonym to be necessary". However, whether or not the name *E. truttaceus* Cuvier (1817) is the result of a misidentified type species, it is *nomen nudum* and therefore has no taxonomic standing. The name *G. truttaceus* Valenciennes is the original name applied to this species, and its application is supported by the presence of syntypes in the Museum National d'Histoire Naturelle, Paris.

Stokell (1966) in seeking a replacement name for *truttaceus* incorrectly classified the junior synonym *G. ocellatus* McCoy (1967) as a *nomen oblitum*. However, since a *nomen oblitum*, prior to changes in the International Code of Zoological Nomenclature in 1972, was an unused senior synonym which endangered nomenclatural stability in the use of a long recognised more junior name, there is no way that *G. ocellatus* McCoy can properly be regarded as a *nomen oblitum* relative to *G. truttaceus*. It is simply a *junior* synonym of *G. truttaceus*.

*Galaxias scopus* Scott (1936) was described from Clarke Island, Bass Strait, and was said to differ from *G. truttaceus* (p. 98) "mainly in the relative positions of the anal and dorsal . . . it at once being distinguished by the origin of the anal being below or very slightly behind the level of the dorsal origin . . . and in the more lavish spotting". Our observations indicate that the anal origin in *G. truttaceus* is usually slightly behind the dorsal origin (predorsal/preanal ratio 93.7-100.6%), and in view of this variation there is no reason to regard *G. scopus* as distinct. Munro (1957b), Stokell (1966) and Andrews (1976) are all of this opinion.

Whitley (1944) described *G. truttaceus hesperius* from Western Australia; he considered it (p. 264) "advisable to provide a distinctive name for the Western Australian form as it differs from the Tasmanian type in fin counts and inasmuch as the pectoral and anal fins do not extend back so far". Material from Western Australia, including the types, a series from the Goodja River and one fish from the Kalgan River indicated that differences between populations in Western Australia and those in the east are very minor. The number of anal fin rays is a little lower in the west, but not as low as the landlocked population in Great Lake, Tasmania (Table 8). The pectoral count is slightly higher (Table 8), and the vertebral count is lower (58.47, compared with 59.44 in the population at Wilsons Promontory, Victoria), but not as low as in Great Lake (58.14 — Table 8). Thus if the Western Australian population is to be given taxonomic recognition on the basis of the few evident differences, so too should the Great Lake population. However, in view of the differences demonstrated between populations in a wide range of galaxiid species, particularly in *G. brevipinnis* Günther (McDowall 1970a, b, present study) and *G. maculatus* (Jenyns) (McDowall 1972), it is suggested that there is little reason to regard the Western Australian population as taxonomically distinct but rather to recognise only that there are small differences between populations on the basis of existing rather meagre information on relatively few specimens. It is possible that the Western Australian population is restricted to freshwaters (like the Great Lake population), and that observed differences between these fish and typically diadromous populations in eastern Australia and Tasmania are related to the elimination of the marine juvenile stage and thus changed environmental conditions experienced during embryonic and larval development.

The landlocked population in Great Lake is likewise treated as an ecological race of *G. truttaceus*; the observed differences, primarily those noted above in the discussion of the status of the Western Australian populations (Tables 8, 9), are relatively minor and may be attributable to the wholly freshwater life cycle.

Andrews (1976) reported a further landlocked population in Bronte Lagoon, Tasmania, but found nothing supporting separate taxonomic recognition of this population. He also reported a population in a cave stream (Andrews, 1973, 1976), and found (1976: 309) that "In comparison with typical *G. truttaceus* the subterranean population appears to differ only in colouration . . . the characteristic body markings of the species are entirely absent and the background colour is reduced to a uniform pale grey".

Apart from differences noted in the preceding discussion between populations in Western Australia and in Great Lake, differences between populations of *G. truttaceus* are small, as tends to be true of other diadromous galaxiids (McDowall, 1970a).

DIAGNOSIS: Characterised by stout build, growth to a large size, the anal fin origin being only slightly behind the dorsal origin, the presence of dark to black fringes on the dorsal, anal and pelvic fins, of numerous, distinctly round spots each surrounded by a halo on the trunk, and of two (occasionally one) dark, vertical bars just behind and above the pectoral fin base.

*G. truttaceus* most closely resembles *G. auratus,* from which it can be distinguished by its fewer and distinctly round spots on the trunk and its post-pectoral dark bars. It has more dorsal and anal rays, although overlap is broad, and has more vertebrae (56-62, usually 59 or more in *G. truttaceus* compared with 53-56 in *G. auratus*). There are differences in body proportions (Table 9), but overlap is broad.

It also resembles *G. tanycephalus*, but can be distinguished by most of the same characters that are used to distinguish it from *G. auratus*.

DESCRIPTION: A large, stout-bodied species, the trunk tubular anteriorly, becoming compressed at about the pelvic fins, the back somewhat arched, the belly rather more deepened, tapering to a moderately long and deep caudal peduncle, the peduncle somewhat longer than deep. Head of moderate length, broad and deep, breadth about equal to depth. Snout rounded; mouth large, moderately oblique, reaching back behind front of eye, sometimes as far as anterior third. Jaws about equal. Eyes moderate to large, set distinctly below upper head profile, interorbital broad and convex, not flattened dorsally. Jaws with enlarged lateral canine teeth; mesopterygoidal and lingual teeth strong. Gill rakers of moderate length, slender (Fig. 43); pyloric caeca reduced to vestiges (Fig. 45). Laterosensory pores on head as in Fig. 47.

Fins well developed, thick and fleshy at bases. Dorsal and anal fins short-based, high and rounded, posterior rays long, extending well back beyond fin bases. Anal fin origin below or a little behind dorsal origin. Pectoral fins of moderate size, rounded, fin insertion lateral, fin lamina lateral. Pelvic-anal interval short, pelvic fins of moderate size, inserted somewhat behind mid-point of standard length. Caudal fin emarginate to slightly forked, fin tips rounded, fin depth rather less than body depth, caudal peduncle flanges moderately developed.

Variation: meristic: see Table 8
morphometric: see Table 9

COLOUR: Colour when alive brownish to a deep olive-grey, or almost black, sometimes a deep purplish-grey, paling to olive-grey on the sides, and silvery-olive on the belly. The trunk is covered with round spots, these tending to occur in vertical rows, especially anteriorly and in smaller fish, each spot surrounded by a paler halo. There is a distinct, dark, blue-black post-pectoral bar separated from a second, similar bar by a narrow, pale vertical line, the second bar sometimes fragmented to form a dense mass of spots. The fins are generally brownish to dark olive, but the dorsal, anal and caudal fins are golden to bright orange on the distal halves; the outer fringes of the dorsal, anal and pelvic fins are black. The eyes are a dark olive-gold. There is a distinct, diagonal, dark stripe passing from the eye backwards and downwards across the cheeks, almost parallel to the heavily pigmented upper lip.

The juvenile "whitebait" stage, at migration upstream from the sea, is very weakly pigmented, with only a few melanophores on the top of the head, along the back and belly and at the base of the tail. Pigmentation develops as a series of melanophores arranged along the myosepta, thus being chevron-shaped, with rather more and large melanophores along the back. Subsequently a series of broader, dark, vertical, straight to slightly chevron-shaped bars develop across the sides of the trunk. With growth, these bars become fragmented, initially in the caudal region, but increasingly so towards the head, the bars initially replaced by vertical series of spots, but the spots ultimately becoming non-linear and more randomly distributed. Scott (1941) has described the ontogenetic changes in colouration of *G. truttaceus* in considerable detail.

SIZE: *G. truttaceus* is one of the largest galaxiids, reaching a reported maximum size of 172 mm S.L. (about 197 mm L.C.F.) (Andrews, 1976). Andrews (p. 307) reported that "most populations sampled yielded individuals within the range 100-120 mm S.L.". (120-137 mm L.C.F.) Specimens about this size are common in collections.

HABITAT: *G. truttaceus* occurs in rivers and streams, mostly amongst cover at the margins. It was taken around the shore of Great Lake from amongst submerged terrestrial vegetation, and from beneath debris and rocks on the lake bed. It appears to be largely a species of still to gently flowing waters, although its ability to move upstream is greater than that of *G. maculatus,* which is mostly confined to waters not far inland. Salinity tolerances were demonstrated by Scott (1941:59) who showed that the fish tolerated "direct transference from tap water to sea water of salinity 35 gm per 1000 gm; in no instance has the fish manifested any noteworthy symptoms of distress".

LIFE HISTORY: *G. truttaceus* has long been known to have a marine juvenile phase (Scott, 1941: Blackburn, 1950). Specimens were taken from the sea by Andrews (1976). The young make their way upstream from the sea during the spring and summer at a length of between about 45 mm and 65 mm L.C.F. The shoals of juveniles move into fresh

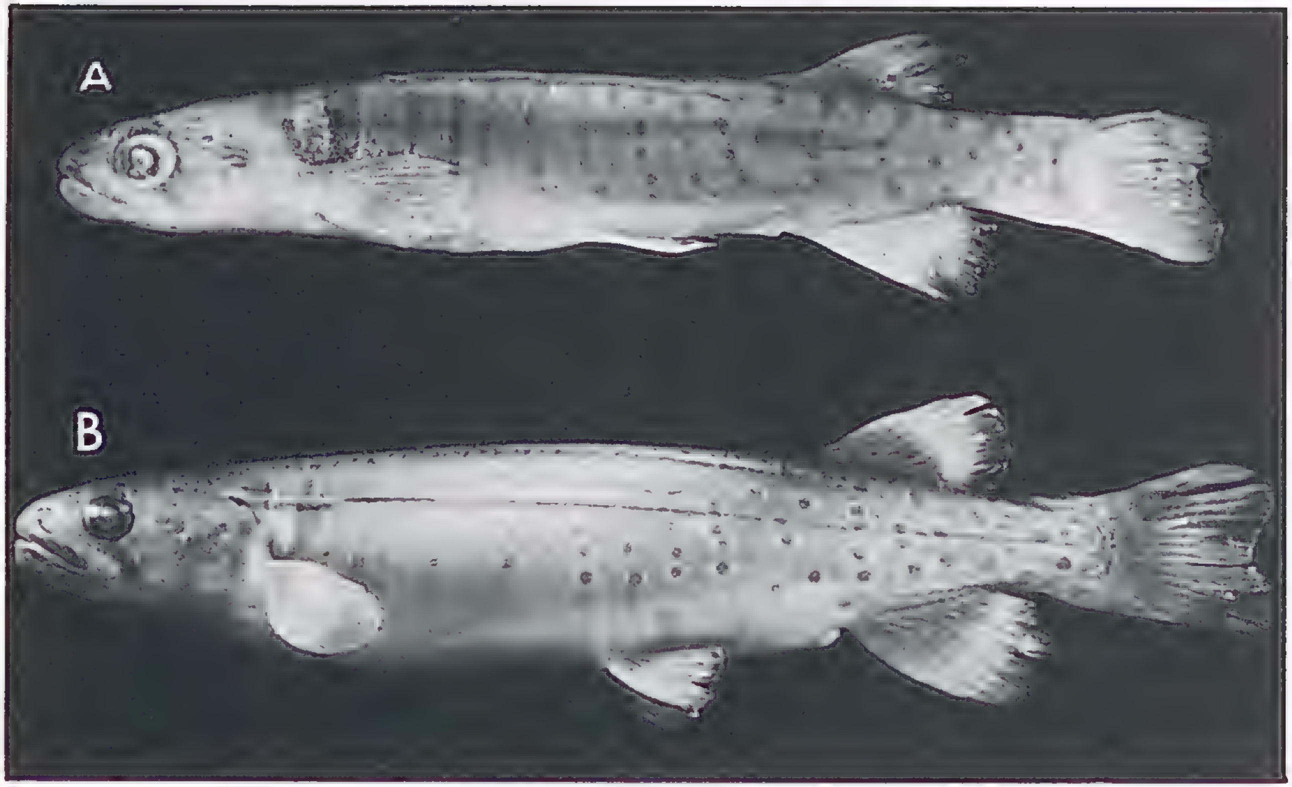

Fig. 15. Variation in colour pattern in *Galaxias truttaceus;* **a.** Shelly Beach, Vic., 63 mm L.C.F.; **b.** Nubeena, Tas., 150 mm L.C.F.

Table 8. Meristic variation in *Galaxias truttaceus, G. auratus* and *G. tanycephalus*.

| | | *G. truttaceus* | | | | | | | | | *G. auratus* | *C. tanycephalus* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Shelley Beach Otways, Vic. | Wilsons Promontory, Vic. | King Island | Flinders Island | Wynyard Tasmania | Dover Tasmania | Cox Bright Tasmania | Great Lake Tasmania | Western Australia | Lakes Sorell & Crescent | Arthurs & Woods Lakes |
| Dorsal rays — segmented | 7 | | | | | | | | | | 2 | |
| | 8 | | | | | | | | | | 10 | 3 |
| | 9 | | | 4 | | | | 3 | | 3 | 10 | 13 |
| | 10 | 8 | | 6 | 8 | | | 5 | | 5 | 1 | 4 |
| | 11 | 2 | | | 2 | | | 2 | | 2 | | |
| total | 9 | | | | | | | | | | 1 | |
| | 10 | | | | | | | | | | 2 | |
| | 11 | | | 3 | | | | | 1 | | 9 | 11 |
| | 12 | 3 | | 2 | | 1 | 1 | 4 | 15 | 6 | 2 | 8 |
| | 13 | 5 | 4 | 5 | 8 | 7 | 7 | 6 | 6 | 11 | 4 | 1 |
| | 14 | 1 | 5 | | 15 | 16 | 5 | | | 3 | | |
| | 15 | 1 | | | 1 | 1 | 2 | | | | | |
| Anal rays — segmented | 11 | | | | | | | | | | 10 | 8 |
| | 12 | 1 | | 3 | 1 | | | 2 | | 5 | 10 | 12 |
| | 13 | 5 | | 5 | 6 | | | 4 | | 4 | | |
| | 14 | 3 | | 2 | 3 | | | 4 | | 1 | | |
| | 15 | 1 | | | | | | | | | | |
| total | 13 | | | | | | | | | | 1 | 2 |
| | 14 | | | | | | | | 6 | 1• | 13 | 8 |
| | 15 | 1 | | | 1 | | | 1 | 9 | 4 | 20 | 9 |
| | 16 | 2 | 1 | 5 | 2 | 3 | 6 | 3 | 6 | 14 | 6 | 1 |
| | 17 | 4 | 6 | 4 | 9 | 16 | 6 | 3 | | 4 | | |
| | 18 | 3 | 2 | 1 | 12 | 6 | 2 | 3 | | | | |
| | 19 | | | | | | 1 | | | | | |
| Pectoral rays | 13 | | 1 | | 2 | | | 1 | | 1 | | |
| | 14 | 5 | 5 | 4 | 10 | 7 | 7 | 3 | 10 | 4 | 1 | 2 |
| | 15 | 5 | 3 | 6 | 10 | 14 | 8 | 5 | 11 | 13 | 20 | 10 |
| | 16 | | | | 2 | 4 | | 1 | 1 | 2 | 15 | 7 |
| | 17 | | | | | | | | | | 1 | 1 |
| | 18 | | | | | | | | | | 1 | |
| Gill rakers | 13 | 1 | | | | | | 3 | | | | |
| | 14 | 6 | | 4 | 2 | | | 2 | | | | |
| | 15 | 2 | | 5 | 6 | | | 3 | | 1 | | |
| | 16 | 1 | | 1 | 2 | | | 1 | | 5 | 1 | 1 |
| | 17 | | | | | | | 1 | | 4 | 3 | 7 |
| | 18 | | | | | | | | | | 5 | 5 |
| | 19 | | | | | | | | | | 8 | 4 |
| | 20 | | | | | | | | | | 3 | 2 |
| | 21 | | | | | | | | | | | 1 |
| Vertebrae | 53 | | | | | | | | | | 1 | 2 |
| | 54 | | | | | | | | | | 13 | 6 |
| | 55 | | | | | | | | | | 5 | 16 |
| | 56 | | | | | | | | 2 | | 1 | 5 |
| | 57 | | | | | | | | 1 | | | |
| | 58 | | 1 | | | 1 | | | 12 | 10 | | |
| | 59 | | 4 | 1 | | 2 | 4 | | 6 | 6 | | |
| | 60 | | 3 | 3 | 11 | 9 | 8 | | 1 | 1 | | |
| | 61 | | 1 | 2 | 12 | 12 | 3 | | | | | |
| | 62 | | | | 1 | | | | | | | |

Table 9. Morphometric variation in *Galaxias truttaceus, G. auratus,* and *G. tanycephalus.* Figures are given as percentages of denominators in ratios.

| | | S.L./T.L. | B.D.V./S.L. | L.C.P./S.L. | D.C.P./L.C.P. | Pre D/S.L. | Pre D/Pre A | L.D.B./S.L. | M.L.D./L.D.B. | L.A.B./S.L. | M.L.A./L.A.B. | Pec/PecPel |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *G. truttaceus* | | | | | | | | | | | | |
| Shelly Beach, Victoria | Mean | 87.63 | 17.34 | 12.54 | 79.67 | 73.28 | 98.33 | 10.93 | 175.14 | 15.34 | 141.72 | 52.70 |
| | S.D. | 0.96 | 0.85 | 0.70 | 6.21 | 1.30 | 1.16 | 0.63 | 10.46 | 0.73 | 9.93 | 4.70 |
| Rhodes Creek, Kangaroo Island | Mean | 87.00 | 17.17 | 13.13 | 75.41 | 71.70 | 96.96 | 10.72 | 182.60 | 14.87 | 149.25 | 55.54 |
| | S.D. | 0.66 | 0.82 | 0.68 | 5.20 | 1.28 | 1.82 | 0.56 | 8.52 | 0.61 | 4.90 | 3.73 |
| King Island, Bass Strait | Mean | 87.31 | 17.98 | 12.97 | 79.07 | 72.83 | 98.48 | 10.50 | 180.32 | 14.75 | 147.20 | 51.39 |
| | S.D. | 0.71 | 1.02 | 0.38 | 4.29 | 1.23 | 1.32 | 0.70 | 11.99 | 0.53 | 4.42 | 4.05 |
| Cox Bight, Tasmania | Mean | 87.51 | 16.32 | 15.84 | 73.46 | 73.30 | 97.11 | 10.61 | 174.91 | 15.15 | 141.55 | 54.87 |
| | S.D. | 0.87 | 1.02 | 1.48 | 6.74 | 0.66 | 0.78 | 0.93 | 17.51 | 0.93 | 8.55 | 4.84 |
| Nanarup, Western Australia | Mean | 86.91 | 15.61 | 13.47 | 70.00 | 72.28 | 96.84 | 10.12 | 175.44 | 13.56 | 144.67 | 51.12 |
| | S.D. | 0.52 | 0.74 | 0.84 | 5.33 | 1.23 | 2.14 | 0.58 | 12.54 | 0.65 | 9.15 | 5.17 |
| Great Lake, Tasmania | Mean | 87.10 | 16.05 | 14.95 | 60.85 | 73.15 | 98.18 | 10.10 | 172.60 | 12.45 | 152.28 | 53.63 |
| | S.D. | 0.38 | 0.79 | 0.88 | 1.89 | 0.97 | 0.88 | 0.24 | 3.32 | 0.65 | 7.48 | 4.02 |
| All data | Min | 85.8 | 13.7 | 11.8 | 59.5 | 70.01 | 93.7 | 9.4 | 146.7 | 11.6 | 130.3 | 42.9 |
| | Mean | 87.26 | 16.82 | 13.69 | 74.44 | 72.71 | 97.59 | 10.54 | 177.31 | 14.56 | 145.53 | 54.11 |
| | Max | 89.3 | 19.4 | 15.9 | 88.7 | 75.1 | 100.6 | 12.6 | 211.1 | 16.7 | 163.0 | 63.3 |
| *G. auratus* | Min | 86.8 | 14.9 | 10.8 | 68.3 | 71.5 | 90.9 | 7.4 | 180.0 | 10.8 | 147.7 | 41.8 |
| | Mean | 88.26 | 16.29 | 12.49 | 77.51 | 73.60 | 93.53 | 8.59 | 197.41 | 12.37 | 157.99 | 47.26 |
| | Max | 89.8 | 18.6 | 13.6 | 87.1 | 76.3 | 96.8 | 9.8 | 225.0 | 13.8 | 176.9 | 50.7 |
| | S.D. | 0.72 | 0.96 | 0.65 | 5.43 | 1.16 | 1.56 | 0.74 | 11.09 | 0.88 | 8.12 | 2.88 |
| *G. tanycephalus* | Min | 86.7 | 13.3 | 12.9 | 48.1 | 68.8 | 94.1 | 8.1 | 125.0 | 10.6 | 125.0 | 37.8 |
| | Mean | 89.13 | 14.53 | 15.03 | 56.58 | 71.89 | 96.46 | 9.56 | 159.28 | 12.54 | 136.98 | 47.48 |
| | Max | 91.1 | 15.8 | 16.7 | 72.0 | 74.6 | 99.1 | 11.4 | 181.0 | 13.3 | 161.0 | 54.2 |
| | S.D. | 1.06 | 0.76 | 1.06 | 6.39 | 1.63 | 1.49 | 0.91 | 14.69 | 0.82 | 9.45 | 3.91 |

| Pel/Pel An | PrePel/S.L. | PecPel/S.L. | Pel An/S.L. | H.L./S.L. | H.W./H.L. | H.D./H.L. | Sn.L./H.L. | P.O.H.L./H.L. | I.O.W./H.L. | E.D./H.L. | L.U.J./H.L. | L.L.J./H.L. | W.G./H.L. | N |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 61.85 | 54.38 | 30.45 | 21.40 | 25.54 | 59.96 | 60.35 | 32.79 | 50.34 | 42.46 | 21.57 | 42.11 | 39.44 | 35.76 | 10 |
| 4.11 | 1.13 | 1.56 | 1.06 | 0.92 | 3.68 | 3.23 | 1.47 | 2.30 | 1.02 | 1.84 | 2.32 | 2.39 | 2.84 | |
| 60.90 | 52.49 | 29.70 | 22.89 | 23.82 | 54.03 | 56.82 | 30.11 | 51.58 | 41.67 | 21.65 | 38.90 | 38.45 | 29.80 | 10 |
| 2.02 | 0.85 | 1.23 | 0.93 | 0.61 | 2.52 | 2.61 | 1.66 | 3.31 | 2.69 | 1.57 | 0.98 | 1.04 | 1.99 | |
| 59.54 | 53.43 | 29.95 | 21.77 | 24.82 | 57.96 | 59.80 | 30.43 | 51.16 | 40.65 | 21.96 | 39.27 | 37.67 | 33.27 | 10 |
| 2.47 | 0.93 | 1.22 | 0.96 | 0.73 | 4.38 | 4.30 | 1.76 | 1.29 | 1.70 | 1.61 | 1.99 | 1.21 | 2.54 | |
| 63.37 | 55.00 | 28.81 | 21.30 | 27.12 | 57.11 | 57.96 | 31.82 | 49.63 | 40.93 | 21.53 | 43.03 | 40.75 | 35.37 | 10 |
| 6.19 | 1.34 | 1.39 | 1.37 | 0.96 | 3.01 | 2.45 | 1.56 | 1.86 | 1.48 | 1.87 | 1.85 | 2.48 | 3.02 | |
| 56.17 | 52.07 | 28.84 | 23.27 | 25.44 | 54.98 | 54.55 | 29.80 | 50.84 | 39.61 | 21.46 | 39.17 | 37.43 | 31.57 | 10 |
| 3.94 | 1.29 | 1.71 | 1.01 | 1.08 | 3.55 | 3.42 | 1.99 | 2.52 | 1.71 | 2.22 | 2.88 | 2.19 | 3.67 | |
| 62.45 | 53.95 | 29.70 | 20.83 | 26.03 | 57.73 | 56.58 | 33.23 | 48.68 | 38.23 | 18.55 | 39.20 | 36.43 | 32.13 | 4 |
| 4.26 | 1.53 | 1.78 | 1.07 | 2.14 | 2.55 | 1.63 | 1.24 | 2.07 | 2.13 | 1.99 | 2.41 | 2.49 | 2.14 | |
| 51.1 | 50.6 | 26.2 | 19.1 | 23.0 | 48.8 | 48.8 | 26.7 | 48.8 | 37.2 | 15.9 | 35.6 | 34.1 | 24.4 | |
| 60.52 | 53.51 | 29.56 | 22.03 | 25.40 | 56.88 | 57.80 | 31.16 | 50.56 | 40.78 | 21.41 | 40.40 | 38.58 | 33.08 | 54 |
| 72.1 | 57.7 | 32.6 | 24.9 | 29.2 | 67.3 | 65.8 | 35.4 | 54.9 | 47.6 | 25.0 | 46.6 | 45.0 | 42.5 | |
| 52.8 | 52.8 | 29.8 | 19.3 | 24.9 | 50.8 | 52.5 | 26.9 | 50.8 | 33.1 | 16.2 | 30.0 | 29.9 | 27.5 | |
| 57.14 | 57.82 | 31.65 | 21.73 | 26.56 | 56.05 | 56.38 | 29.24 | 54.03 | 35.99 | 17.85 | 33.96 | 32.88 | 30.79 | 20 |
| 67.5 | 60.3 | 34.1 | 22.8 | 28.6 | 61.5 | 60.0 | 31.8 | 57.2 | 38.3 | 20.0 | 36.7 | 36.6 | 35.2 | |
| 3.38 | 1.72 | 1.44 | 1.01 | 0.92 | 2.59 | 2.23 | 1.33 | 1.77 | 1.31 | 1.06 | 1.65 | 1.72 | 2.22 | |
| 59.0 | 53.5 | 28.3 | 17.3 | 24.6 | 46.7 | 49.2 | 29.2 | 50.0 | 30.1 | 15.0 | 31.0 | 31.0 | 24.8 | |
| 64.07 | 55.80 | 30.69 | 19.60 | 26.98 | 51.52 | 52.54 | 32.47 | 52.57 | 33.94 | 19.53 | 35.71 | 34.98 | 27.16 | 20 |
| 79.5 | 58.2 | 33.3 | 22.7 | 31.9 | 57.9 | 56.5 | 35.1 | 55.2 | 36.7 | 21.1 | 40.0 | 36.9 | 29.2 | |
| 4.76 | 1.51 | 1.25 | 1.26 | 1.70 | 3.04 | 2.32 | 1.67 | 1.55 | 2.06 | 1.55 | 1.97 | 1.40 | 1.16 | |

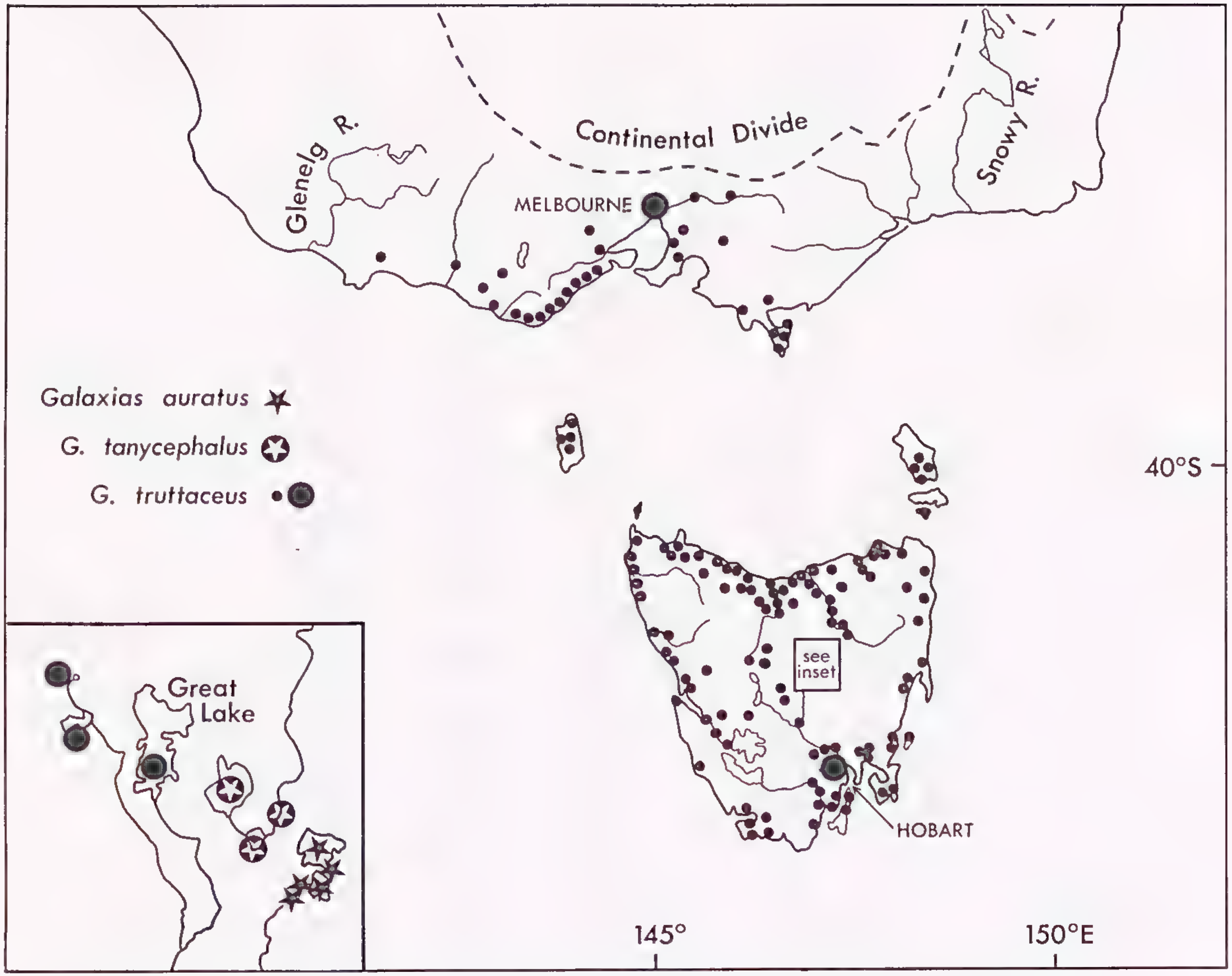

Fig. 16. Distribution of *Galaxias auratus*, *G. tanycephalus* and *G. truttaceus* (Eastern Australia). One symbol may represent more than one locality.

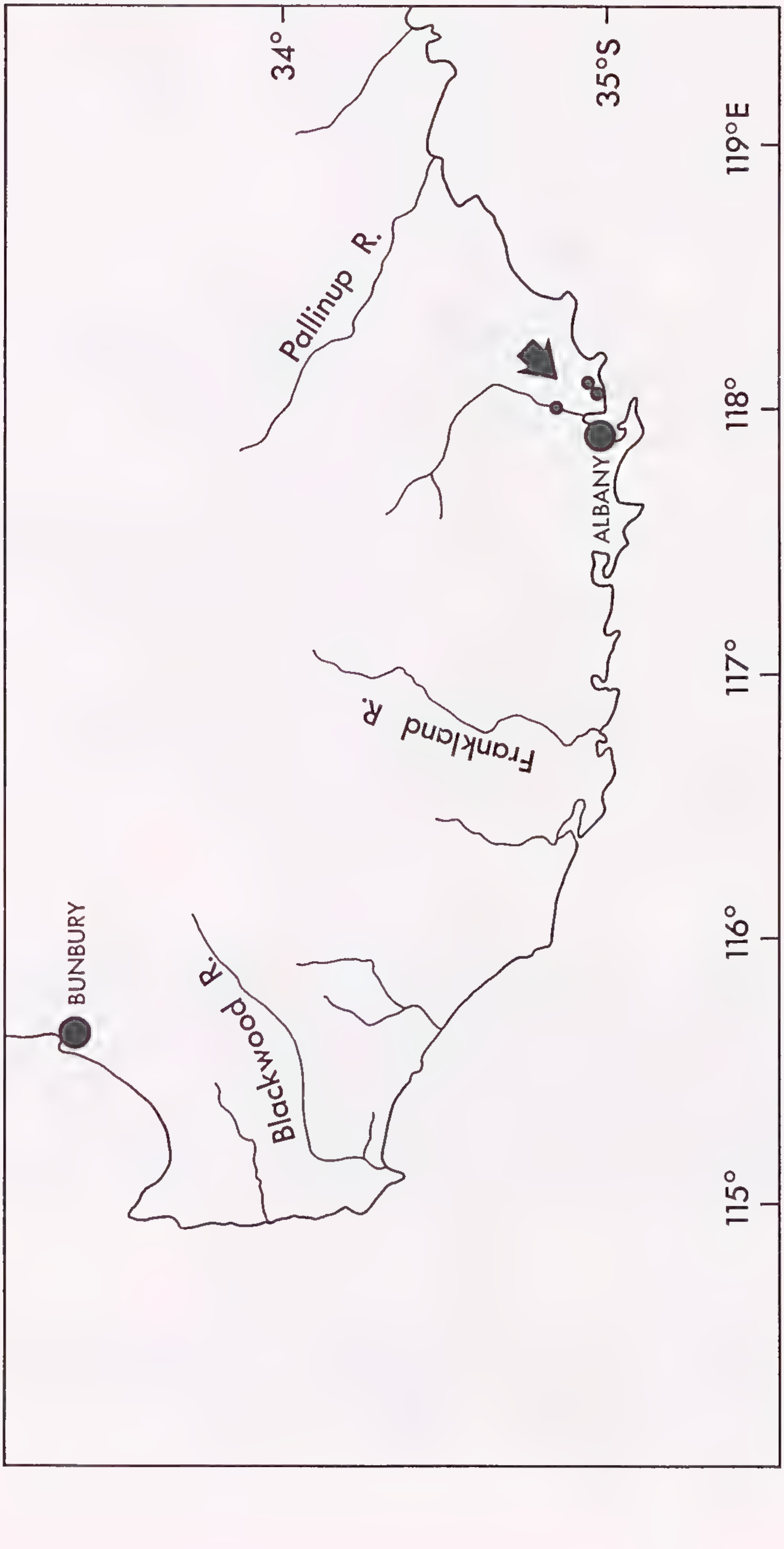

Fig. 17. Distribution of *Galaxias truttaceus* (Western Australia).

water where they grow, passing through the colour phases discussed above ("Colour"); at the same time they become much more stoutly built, soon attaining the generally stocky build of the adults. Both Scott (1941) and Andrews (1976) reported spawning during the autumn, Scott stating that a fish of 113 mm S.L. (129 mm L.C.F.) carried 5634 ova 1.0-1.3 mm in diameter. Thus the eggs like those of most diadromous galaxiids are relatively small and numerous (McDowall, 1970a). Nothing is known of spawning behaviour or the whereabouts of the eggs when laid, although Scott (1941: 68) speculated that "it seems not unlikely that, where circumstances permit, this species migrates to brackish water, possibly even to the sea to spawn". The truth of this remains unconfirmed from observation.

The population in Great Lake once had freedom to move downstream and the young to move upstream into the lake from the river system draining the lake. Since closure of the outflow of Great Lake through the Shannon River and the Derwent River to the sea by construction of a dam in 1916 movement to and from Great Lake has been prevented; the population in the lake has thus eliminated the marine life history phase. This is known to have occurred in landlocked stocks of several other diadromous species, e.g. *G. maculatus, G. fasciatus, G. brevipinnis* (McDowall, 1970a, 1972).

DISTRIBUTION: *G. truttaceus* is known from southern Victoria, King, Flinders and Clarke Islands in Bass Strait, from Tasmania, and from a very restricted area in the south of Western Australia (Fig. 16, 17). Apart from the moderate altitude inland populations in Great Lake, Julian Lakes, and Bronte Lagoon, Tasmania, it is found primarily at low elevations and close to the sea.

Scott, Glover and Southcott (1974: 77) report this species from South Australia, stating that it is "not common in our State, but is occasionally found in the mountain rivers and streams". We have been unable to authenticate any records of *G. truttaceus* from South Australia, and believe that the species involved is *G. brevipinnis*, which these authors do not record from South Australia, although it is present and occurs in collections in the South Australian Museum.

### **Galaxias auratus** Johnston

Fig. 18, 19

*Galaxias auratus* Johnston, 1883: 131 (holotype: unknown; type locality: "the neighbourhood of Great Lake at an altitude of about 4,000 feet", Tasmania — the type locality is sometimes stated to be Great Lake, but *G. auratus* does not occur in Great Lake, and the type locality is probably Lake Sorell, see Whitley, 1929; Andrews, 1976); Seal et al. 1883; lvi; Macleay, 1886: 56; Johnston, 1891: 27; Anderson, 1900: 25; Regan, 1905: 379; Lord, 1923: 63; Lord and Scott, 1924: 33; Lord, 1927: 12; Whitley, 1929: 47; McCulloch, 1929: 48; Whitley, 1956a: 30; 1956b: 39; 1957a: 7; 1957b: 8; Munro, 1957b: 16; Whitley, 1964: 35; Frankenberg, 1966a: 162; 1966b: 23; Scott, 1968: 7; Lynch, 1972: 8; Andrews, 1973: 104; Frankenberg, 1974: 119; Andrews, 1976: 309; Fulton, 1978: 114; Lake, 1978: 22.

*Galaxias (Galaxias) auratus* — Scott, 1936: 91.

TAXONOMY: There are no taxonomic problems associated with the identity and nomenclature of *G. auratus*. Only two populations are known and the population in Lake Crescent was derived (when the lake was formed by man) from that in Lake Sorell; no comparisons between the populations were made. *G. auratus* is clearly distinct from *G. truttaceus,* which it most closely resembles.

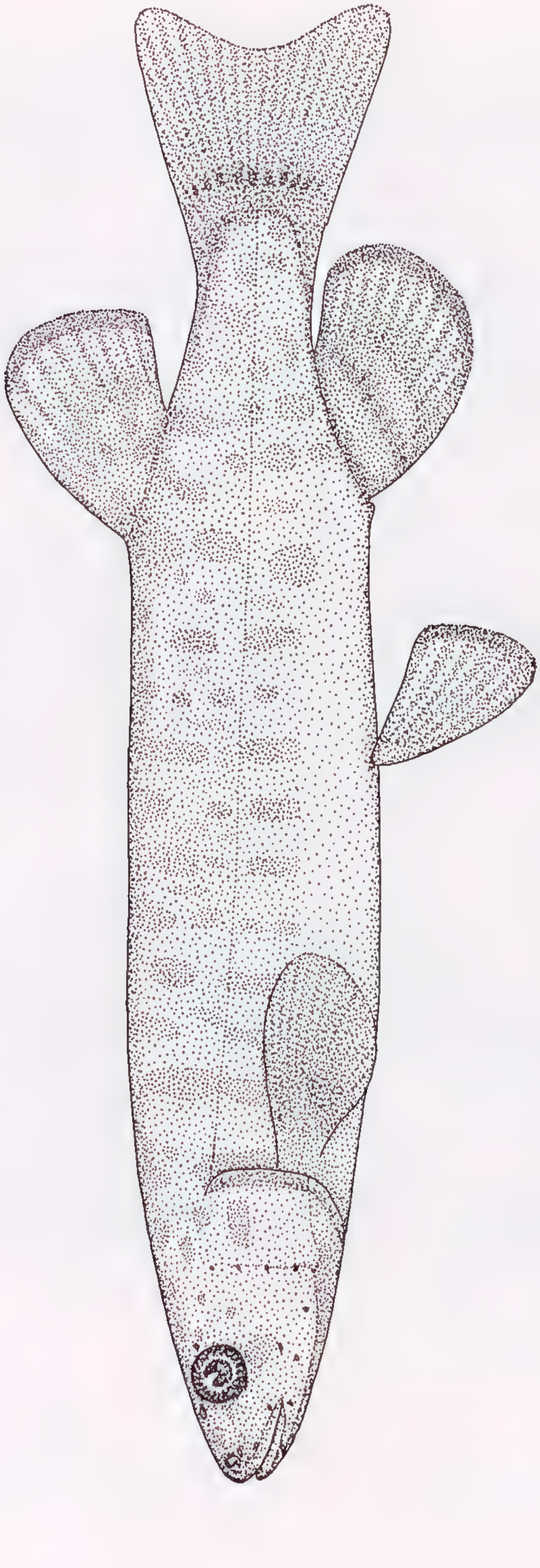

Fig. 18. *Galaxias auratus* Johnstone; Lake Crescent, Tas., 123 mm L.C.F.

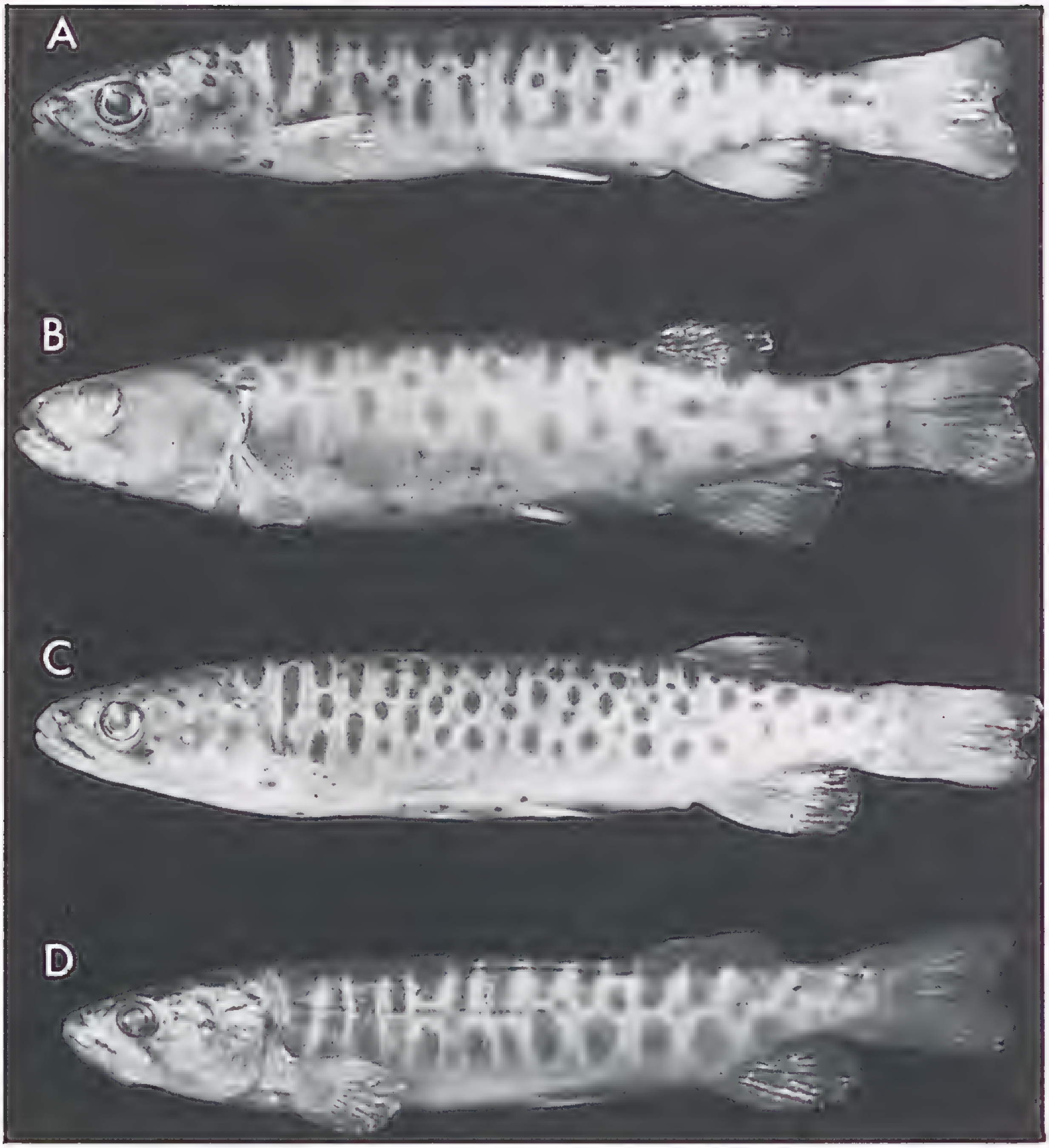

Fig. 19. Variation in colour pattern in *Galaxias auratus;* **a.** 73.5 mm L.C.F.; **b.** 80 mm L.C.F.; **c.** 103 mm L.C.F.; **d.** 118.5 mm L.C.F.; all specimens from Lake Crescent, Tas.

DIAGNOSIS: Characterised by moderate to large size, somewhat compressed form (although generally stout) and golden colour when alive. It differs from *G. truttaceus* and *G. brevipinnis* in characters discussed in the diagnoses of these two species (pp.504 and 462 respectively). It differs from *G. tanycephalus* in being generally stouter, with a shorter, deeper caudal peduncle, broader and deeper head, wider gape, smaller dorsal and anal fins, and in colouration.

DESCRIPTION: A large stout-bodied species, the trunk slightly compressed from behind the head, becoming more compressed on caudal peduncle, dorsal and ventral trunk profiles slightly and evenly arched; somewhat depressed anteriorly on head. Caudal peduncle short and deep, a little longer than deep. Head of moderate length, about as deep as broad, flattened dorsally. Snout long tapering to a rounded point. Mouth moderately oblique, reaching back to about front of eyes, jaws sub-equal. Eyes small, set below dorsal head profile, interorbital convex, dorsally flattened. Jaws with enlarged canine teeth laterally; mesopterygoidal and lingual teeth well developed. Gill rakers of moderate length, stout (Fig. 43). Pyloric caeca reduced to one or two weak shoulders or lacking (Fig. 45). Laterosensory pores on head as in Fig. 47.

Fins well developed, somewhat fleshy at bases. Dorsal and anal fins short-based but high and rounded, posterior rays extending well back beyond fin bases; anal origin set back a little from dorsal origin. Pectoral fins small and rounded, lateral to latero-ventral, fin lamina more or less vertical. Pelvic-anal interval short, pelvic fins of moderate size, inserted well behind mid-point of standard length. Caudal fin emarginate, fin tips rounded, fin depth rather less than body depth; caudal peduncle flanges moderately developed.

Variation: meristic: see Table 8
morphometric: see Table 9.

COLOUR: Colour when alive gold to olive-green on the back paling to bronze-gold on the sides and silvery-grey on the belly, the back and sides profusely covered with vertical grey-olive to black bands in smaller fish, these bands becoming fragmented to form a series of roundish spots along the back and distinctly oval spots along the sides in two series, one above and one below the lateral line, sometimes a series of much smaller, round spots along the lateral line; Andrews (1976: 311) described the bars and spots on the sides as "reddish-purple". The fins are amber to distinctly pinkish-orange, the fringes of the dorsal, anal and pelvic fins being black. The eyes are silvery-olive.

In preservation it is a dull buff-brown, the spots darker brown, the belly a paler buff; the fringes of the dorsal, anal and pelvic fins are black. The colour pattern varies with growth. Juveniles less than about 50 mm L.C.F. have about 10 more or less distinct vertical bars. As the fish grow these bars break up into vertical rows of oval spots which become increasingly circular. In some fish the bars and spots are surrounded by distinct, paler halos.

SIZE: *G. auratus* is one of the larger galaxiids, reaching at least 237 mm L.C.F. (Johnston, 1883); the largest we have seen was 230 mm L.C.F. It commonly reaches 130-140 mm L.C.F.

HABITAT: *G. auratus* occurs in lakes and associated streams and rivers, forming shoals in open water when small, the larger ones tending to move into cover around the margins. It is essentially a still water species.

LIFE HISTORY: Andrews (1976) reported that he found post larval specimens in December, and concluded that spawning takes place in winter or early spring. This was supported by his collection of adults with immature gonads in January-March. Juveniles 40-45 mm L.C.F. are chunky little fishes, quite unlike the migratory "whitebait" juveniles of *G. truttaceus*.

Unlike many galaxiids, *G. auratus* seems to have been little affected by the introduction of trout; it forms an important food for trout in Lakes Sorell and Crescent, but remains very abundant in both lakes.

DISTRIBUTION: *G. auratus* occurs only in Lake Sorell (Fig. 16), Lake Crescent, a tributary of Lake Crescent at Interlaken, and the Clyde River, which drains Lake Crescent. Lakes Crescent and Sorell, which are on the central plateau of Tasmania southeast of Great Lake, are connected by a canal and it seems likely that the fish invaded Lake Crescent from Lake Sorell, through this canal.

### **Galaxias tanycephalus** Fulton

Fig. 20, 21

*Galaxias tanycephalus* Fulton, 1978: 110 (holotype: TMH D.1266, seen; paratypes: (3) TMH D.1267-9; (2) QVML 1976/5/183 (type 227); (3) AMS I.19334-001; type locality: from amongst rocks around the shore near pumping station, Arthurs Lake, Tasmania); McDowall and Fulton, 1978: 106; Lake, 1978: 22.

TAXONOMY: *G. tanycephalus* is only recently described and no taxonomic discussion is necessary; only one population is known.

DIAGNOSIS: Characterised by relatively stout, but tapering build, large mouth, the gape reaching to about margin of small eye, the lower jaw sometimes protruding slightly, the large head, tapering , pointed snout, and the distinctly forked caudal fin. Differs from *G. truttaceus* and *G. auratus* in characters discussed in the diagnoses of these two speices (pp.504 and 515 respectively).

DESCRIPTION: A moderate-sized, bullet-shaped species, the trunk moderately compressed, the back and belly evenly arched, tapering to a short and slender caudal peduncle, the peduncle much longer than deep. Head long, rather slender, a little deeper than broad. Snout long and pointed, mouth large, moderately oblique, reaching back to about front of eye. Jaws equal or lower protruding slightly. Eyes small, set a little below upper head profile, interorbital broad and slightly convex. Jaws with slight enlargement of canine teeth laterally; mesopterygoidal and lingual teeth strong. Gill rakers of moderate length, strong (Fig. 43); pyloric caeca reduced to indistinct shoulders, or lacking (Fig. 45). Laterosensory pores on head as in Fig. 47.

Fins small somewhat thick and fleshy at bases. Dorsal and anal fins short-based, high and rounded, posterior rays long, the fins extending well back beyond fin bases. Anal fin origin a little behind dorsal origin. Pectoral fins small, paddle-shaped, insertion lateral, fin lamina vertical. Pelvic fins also small, inserted distinctly behind mid-point of standard length. Caudal fin distinctly forked, fin tips rounded, fin depth less than body depth, caudal peduncle flanges well developed but not extending far forwards on peduncle.

Variation: meristic: see Table 8.
morphometric: see Table 9.

COLOUR: Colour when alive grey-black to green-olive on the back with saddle-like greyish bars across the back and sides, the belly silvery-olive. There is a distinct purplish sheen along the sides in some specimens, and some are spotted rather than barred. Small fish have broad irregular blotches on the back and sides. The fins are olive to amber, usually lacking black fringes (cf. *G. truttaceus* and *G. auratus*).

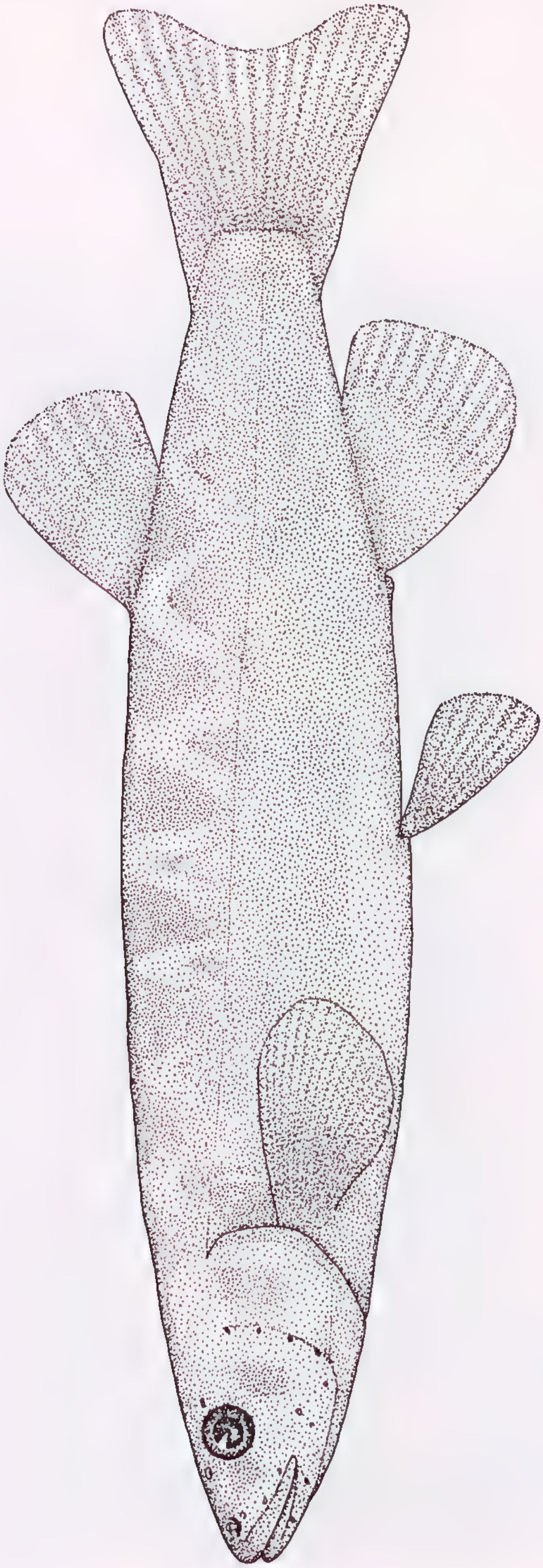

Fig. 20. *Galaxias tanycephalus* Fulton; Arthurs Lake, Tas., 123 mm L.C.F.

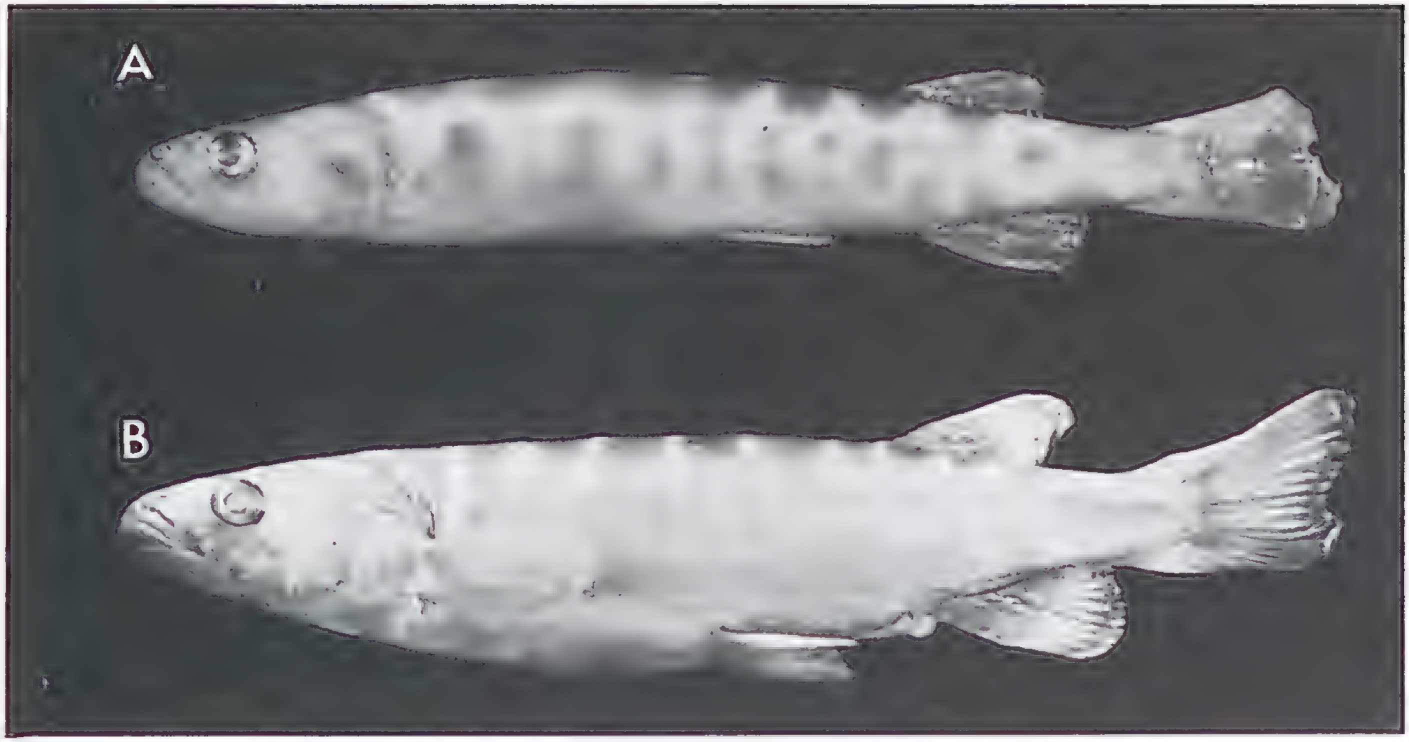

Fig. 21. Variation in colour pattern in *Galaxias tanycephalus;* **a.** 68 mm L.C.F.; **b.** 105 mm L.C.F.; both from Arthurs Lake, Tas.

In preservative, greyish-brown with a row of large ovoid blotches dorso-laterally, extending down about as far as lateral line, the blotches surrounded by paler halos and giving the saddle-like appearance; lower sides dull grey and the belly greyish-white. The fins are dusky at the bases.

SIZE: *G. tanycephalus* is known to reach 147 mm L.C.F., although few fish have been collected and most of these are less than 70 mm L.C.F.

HABITAT: This species was collected from amongst rocks and boulders of man-made groynes around the margins of Arthurs Lake, and seldom from amongst extensive macrophyte beds adjacent to the groynes.

LIFE HISTORY: Nothing is known about the life history of *G. tanycephalus* although its occurrence only in Arthurs Lake, at considerable altitude and distance from the sea, implies that the entire life cycle is spent in fresh water.

DISTRIBUTION: *G. tanycephalus* is known only from Arthurs Lake on the high elevation central plateau of Tasmania (Fig. 16).

### **Galaxias cleaveri** Scott

Fig. 22

*Galaxias cleaveri* Scott, 1934: 44 (holotype: formerly QVML HT.983, now lost; type locality: West Ulverstone, northwest coast, Tasmania); 1935: 45; McDowall, 1970a: 427; Green, 1974: 2; Andrews, 1976: 327; Lynch, 1977: 13; McDowall, 1978c: 208; Lake, 1978: 21.

*Saxilaga (Saxilaga) cleaveri* — Scott, 1936: 106; 1938: 120; 1941: 60.

*Saxilaga (Saxilaga) auguilliformis* Scott, 1936: 106 (holotype: QVML HT.951, seen; paratype: (1) BMNH 1966.5.6:2, not seen; type locality: Cox's Creek, running into Inglis River at Wynyard, northwestern Tasmania); 1938: 121; 1941: 60.

*Galaxias (Galaxias) upcheri* Scott, 1942: 51 (holotype: formerly QVML 1940. 361: 1, now lost; paratypes: (1) BMNH 1966.5.6:4, not seen; (6) formerly QVML unregistered, now lost*; type locality: Dover, southeastern Tasmania, in swampy country — Andrews (1976: 328) has added "anabranch of the Dover Rivulet . . . approximately 182 m northeast of the bridge where Beach Road crosses Dover Rivulet", on information supplied by Mr R. R. Upcher, who collected Scott's (1942) specimens.

*Galaxias upcheri* — Whitley, 1956a: 34; 1956b: 39; 1957a: 7; Munro, 1957b: 15; Gentilli, 1961: 488; Whitley, 1964: 35; Lake, 1971: 20; Green, 1974: 3.

*Galaxias anguilliformis* — Stokell, 1945: 113; McDowall, 1970a: 427; 1978c: 208.

*Lixagasa cleaveri* — Whitley, 1956a: 34.

*Saxilaga cleaveri* — Whitley, 1956b: 39; 1957a: 6; 1957b: 10; Munro, 1957a: 18; Whitley, 1960: 30; 1964: 35; Frankenberg, 1966a: 163; 1966b: 22; Scott, 1966: 251; McDowall, 1969: 804; Lake, 1971: 20; Scott, 1971a: 5; Frankenberg, 1974: 114.

*Saxilaga anguilliformis* — Whitley, 1956b: 39; 1957a: 6; Munro, 1957b: 15; Whitley, 1960: 30; 1964: 35; Scott, 1966: 251; McDowall, 1969: 809; Lake, 1971: 20; Scott, 1971a: 8; Green, 1974: 3; Frankenberg, 1974: 114.

TAXONOMY: Three Tasmanian galaxiids, described as *Galaxias cleaveri* Scott (1934), *Saxilaga anguilliformis* Scott (1936), and *Galaxias upcheri* Scott (1942), were united under

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*Scott (1942) advised that he intended sending paratypes to AIM, AMS, and the Museum of Zoology at the University of Michigan, but we can find no evidence that they were ever sent.

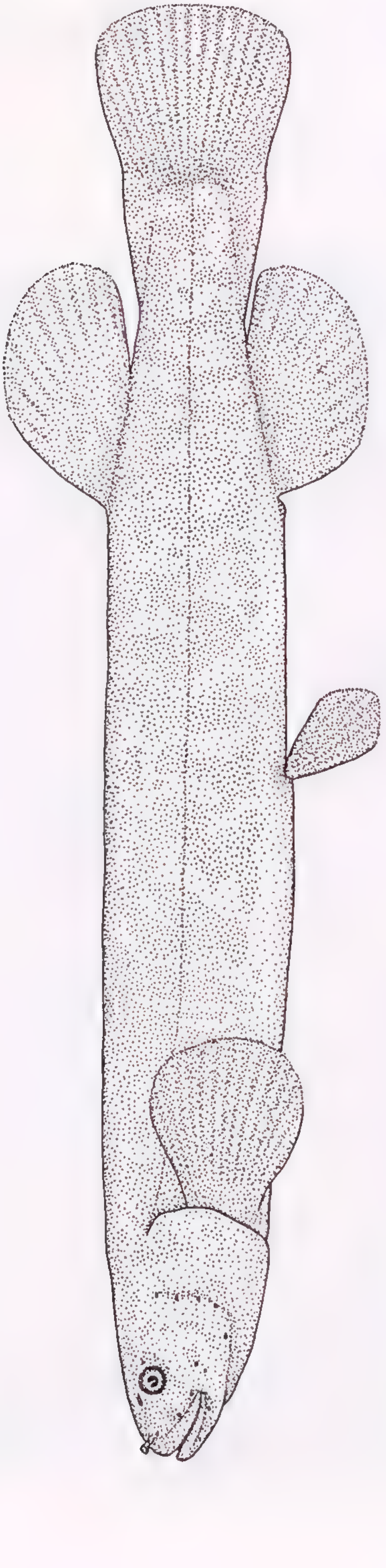

Fig. 22. *Galaxias cleaveri* Scott; Pieman River, Tas., 79 mm T.L.

the senior synonym *G. cleaveri* by Andrews (1976). *G. cleaveri* was originally described on the basis of one specimen (now lost) from West Ulverstone, northwestern Tasmania; *S. anguilliformis* was described from two specimens, from Cox's Creek, Inglis River, northern Tasmania; and *G. upcheri* from eight specimens (all but one lost) from near Dover, southeastern Tasmania. Scott (1936) placed *G. cleaveri* in the genus *Saxilaga* and noted (p. 109) that *S. anguilliformis* differs from *G. cleaveri* "chiefly in having the dorsal and anal rays more numerous and all simple instead of mixed; markedly more forward placed anal . . .; larger eye; shorter snout and perhaps also in the rather stouter body and rather shorter head". *G. upcheri* was distinguished from *G. cleaveri* and *S. anguilliformis* only by having mesopterygoidal teeth and seven-rayed pelvic fins (Scott, 1942).

In his examination of substantially greater numbers of specimens than Scott (1934, 1936, 1942) had studied, Andrews (1976) found that the characters Scott used to distinguish these three species are not diagnostic. Specimens from the north and north-western coasts of Tasmania, which Andrews considered to represent *G. cleaveri* and *S. anguilliformis,* and topotypical material of *G. upcheri,* were found to vary within samples in the number of pelvic fin rays, the presence of mesopterygoidal teeth, and in the presence and number of unbranched rays in the fins. Of most importance, material representing *G. cleaveri* and *S. anguilliformis,* which species Scott (1934, 1936) reported as lacking mesopterygoidal teeth and having only six pelvic fin rays, was shown by Andrews (1976) to vary, with mesopterygoidal teeth either present or absent and pelvic fin rays varying from five to seven, with an overall mean of 6.67 from 30 counts.

Our observations support Andrews' view. Data on 27 specimens showed seven pelvic rays to be present in all but one fish, and that several mesopterygoidal teeth are usually present, although often difficult to see. Material from the northern west coast of Tasmania (Pieman River and Queenstown) which may represent the *G. cleaveri* of Scott (1934, 1936, 1942), samples from the southwest coast (Port Davey), and samples from the southern east coast (Dover), the latter representing *G. upcheri* of Scott (1942), give no indication that more than one species is present. A small sample from Punchbowl Creek, Tamar River, near Launceston in northern Tasmania, differs somewhat from other samples, having slightly lower vertebral counts, longer dorsal and anal fins bases, and slightly larger pectoral and anal fins (Table 10, 11). These differences are not great and the Punchbowl Creek population is also regarded as being *G. cleaveri.*

Inclusion of *G. cleaveri* in the genus *Galaxias,* rather than *Saxilaga,* which is in agreement with Andrews (1976) but at variance with the view of Scott (1936, 1966), is discussed under the definition of the genus *Galaxias* (p.455).

DIAGNOSIS: *G. cleaveri* differs from all other Australian galaxiids in its combination of very small eyes, strongly developed caudal flanges reaching almost to the rear of the very low dorsal and anal fins, very small, paddle-shaped pectoral fins and small pelvic fins, presence of two long pyloric caeca, and long tubular anterior nostrils. The species most likely to cause confusion is *G. parvus,* which has long nostrils, but has no pyloric caeca, has much larger pectoral and pelvic fins (usually more than half of the pectoral-pelvic and pelvic-anal intervals, respectively) and has only three pores in the preopercular series. *G. parvus* is known only from Lake Pedder and its environs and *G. cleaveri* only from lowland localities near the coast.

DESCRIPTION: An elongate, tubular species, the trunk rounded in section, dorsal and ventral trunk profiles parallel tapering somewhat and compressed behind vent. Caudal peduncle short and deep, length a little more than depth. Head short, depth subequal to width, snout bluntly rounded and broad. Mouth moderately oblique and of moderate size, broad, reaching variously to front of eyes or beyond, no further than below middle of eyes, jaws subequal, lower if any a little longer. Eyes very small, upper margins below profile of head, interorbital convex, but eyes sometimes towards upper head profile and interorbital flat. Jaws with slight to moderate development of lateral canine teeth; mesopterygoidal teeth few (sometimes absent); lingual teeth strong; gill rakers short and stout (Fig. 43); two long pyloric caeca (Fig. 45). Laterosensory pores on head as in Fig 47; distinctive in that the anterior pore in the preopercular-suborbital series is usually further forwards than the posterior pore in the supramaxillary series.

Fins small, dorsal and anal fins low and rounded, posterior rays long, the fins extending back moderately beyond fin bases; fin bases moderately fleshy; anal fin origin set back a little from dorsal origin. Pectoral fins small and paddle-shaped, insertion clearly lateral, fin lamina vertical. Pelvic fins also very small, inserted at about mid-point of standard length. Caudal fin usually rounded, tending towards truncate; peduncle flanges very strongly developed, more or less confluent with rear of dorsal and anal fin bases.

Variation: meristic: Table 10.
morphometic: see Table 11.

COLOUR: Described, in life, by Andrews (1976: 328) as follows: "Uniform dark greenish brown on back and sides with a narrow dark bluish grey unpigmented stripe along the abdominal surface. Bases of dorsal, anal and caudal fins liberally speckled with small dark brown spots, paired fins clear and hyaline." This differs from Scott's (1934) account; Scott (p. 45) reported the sides "heavily barred and blotched with dark brown . . . Dorsal surface like lateral surface but with more brown. . . ."

Specimens from Dover were brown to golden-brown, sometimes blackish, the back and sides with profuse, irregular, and very variable grey-brown markings and speckling.

In preservative the back and sides of the head and trunk are covered with fine and profuse dark and pale irregular mottling to vermiculations, these sometimes resolving into irregular, vertical bands which may be irregularly chevron-shaped, particularly in small fish. The mottling extends on to the fleshy bases of the dorsal and anal fins, and on to the tail base. The belly is a paler grey to buff-brown.

SIZE: Andrews (1976) reported that this species reaches 125 mm S.L. (about 141 mm L.C.F.); the largest seen during this study was 119.5 mm L.C.F. with specimens over 80 mm not uncommon.

HABITAT: *G. cleaveri* was first collected (Scott, 1934: 41) from within a cavity in a tree root when a stump was "blown out of the ground by explosives" the locality about 0.5 km from the nearest running water, but in an area where "through the winter there is water lying in ponds close to where the stump stood in swampy ground". Scott (1936:109) reported that *S. anguilliformis* occurred in "swamps near the mouths of the Forth River and the Clayton Rivulet, being known locally as the 'mud-trout'. . . . It is generally found when drains are being cleaned out, and seems to be actually dug out of the mud. In swamps and drains that have completely lost all trace of water they can be found in damp mud. I have often got them by turning over logs and stones where they are to be found in mud" (quoted by Scott from a Major R.E. Smith of Launceston). Habitats described by Scott (1942) for *G. upcheri* in southeastern Tasmania are consistent with the above; Scott (p. 54) quotes Mr R. R. Upcher, who collected the fish "in swampy Titree country . . . in dry periods it can be found thriving in quite thick mud." Scott (1934) demonstrated its ability to survive for many hours in the absence of free water.

*G. cleaveri* resembles the New Zealand species of *Neochanna* (McDowall, 1970a) which are known to live in creeks, drains and swamps and bogs, and which are able to aestivate during periods of drought.

LIFE HISTORY: The life history of *G. cleaveri* is unstudied and virtually unknown; Andrews (1976: 331) reported a female with "almost fully developed eggs of 1.3-1.5 mm diameter," collected during May, "which would indicate a late winter spawning." It seems likely that the entire life cycle is spent in freshwater and there is no evidence of a "whitebait" juvenile.

DISTRIBUTION: *G. cleaveri* is known from low-lying areas along the northern, western and south-eastern coasts of Tasmania (Fig. 23), but is, as yet, not known from the east coast, despite searches for it (Frankenberg, 1974).

### **Galaxias parvus** Frankenberg

Fig. 24

*Galaxias parvus* Frankenberg, 1968: 270 (holotype: TMH D.940, seen; paratypes: (16) NMVM A.392-407, seen; type locality: pond on the east bank of Lake Pedder, about 400 yards south of the stream entering Lake Pedder from Lake Maria — the type locality is now obliterated by the flooding of Lake Pedder and its environs to form a water storage lake); Andrews, 1971: 1; Lake, 1971: 20; Bayly et al., 1972: 46; Dixon, 1972: 121; Lynch, 1972: 14; Johnson, 1972: 23; Andrews, 1973: 106; Frankenberg, 1974: 123; Andrews, 1976: 321; Lynch, 1977: 14; Lake, 1978: 22.

TAXONOMY: There appear, at present, to be no problems related to the taxonomy of *G. parvus;* the species is quite distinct from all other galaxiid species, and has uncertain relationships to them.

Few populations of *G. parvus* are known. However, populations in the Lake Pedder — Serpentine River system have fewer vertebrae, pelvic fin rays and dorsal fin rays than those in the upper Huon River, and are more variable in the number of caudal fin rays Table 10; (Fig. 25). These variations would appear to be the result of mosaic evolution in geographic isolates, and they represent the type of variation evident in other freshwater limited galaxiids, e.g. *Neochanna apoda* Günther and *Galaxias divergens* Stokell, in New Zealand (McDowall, 1970a) and *G. platei* Steindachner in Patagonian South America (McDowall, 1971).

DIAGNOSIS: *G. parvus* is distinctive in its combination of 5-6 pelvic fin rays, a rounded caudal fin, short gill rakers and 44-49 vertebrae. It differs from all other species of *Galaxias* in having only three pores in the preopercular series (usually four spores in other *Galaxias* — Fig. 47).

The elongate tubular, anterior nostrils are characteristic and unusual, although present also in *G. cleaveri*.

DESCRIPTION: A small, stocky species, the trunk tubular, dorsal and ventral profiles about parallel, head a little flattened dorsally, trunk compressed behind caudal peduncle which is long and slender, much longer than deep. Head of moderate length, as deep as broad, snout blunt and rounded. Mouth slightly oblique, of moderate size, extending back to about level of eye or a little further, jaws about equal in length or lower projecting slightly. Eyes of moderate size, towards upper head profile, interorbital flat. Jaws without lateral canines. Mesopterygoidal teeth well developed; gill rakers short and stout (Fig. 43); pyloric caeca lacking (Fig. 45); anterior tubular nostrils very long, projecting forwards over upper lip; only three laterosensory pores in preopercular series (Fig. 47).

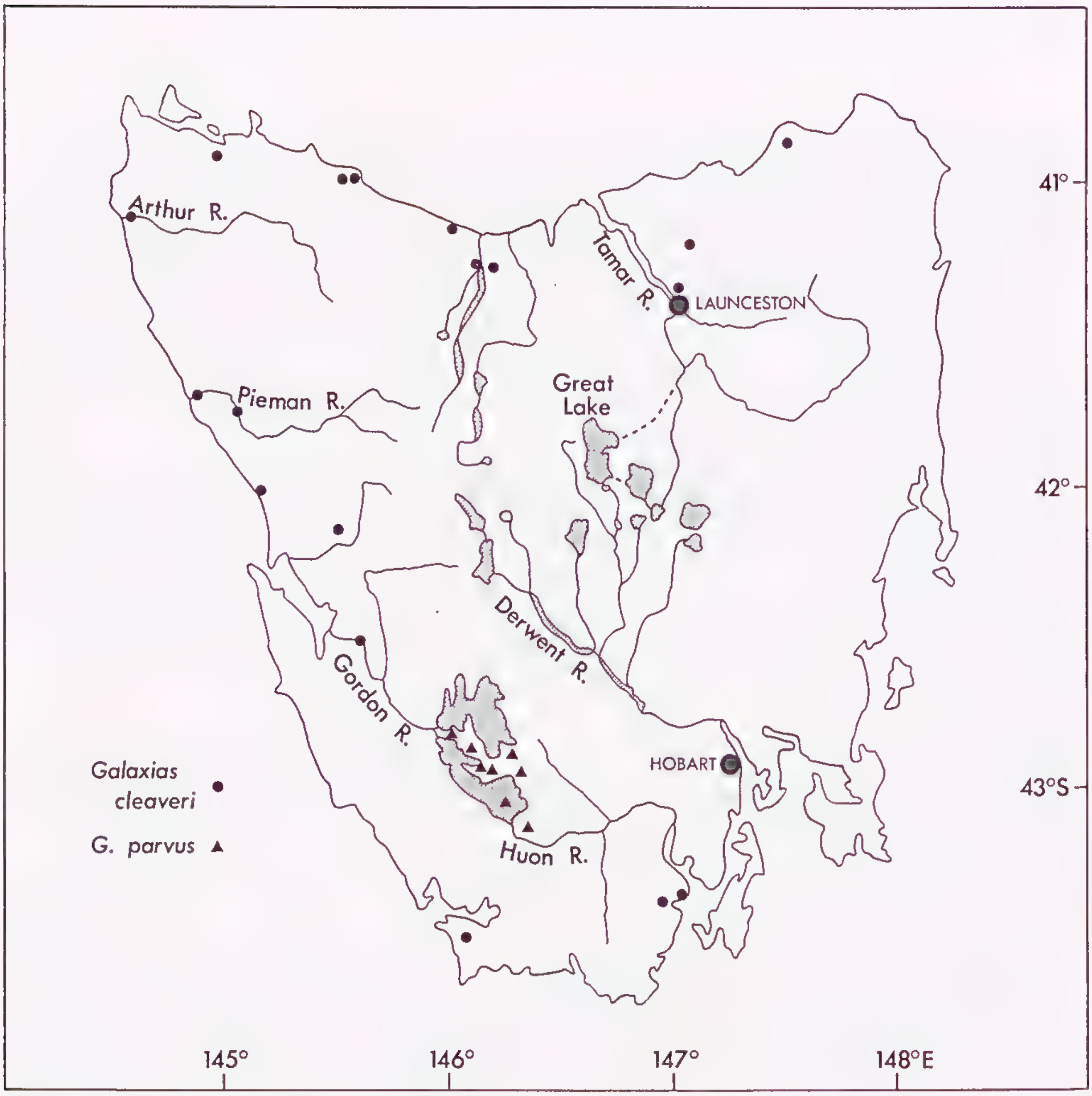

Fig. 23. Distribution of *Galaxias cleaveri* and *G. parvus*.

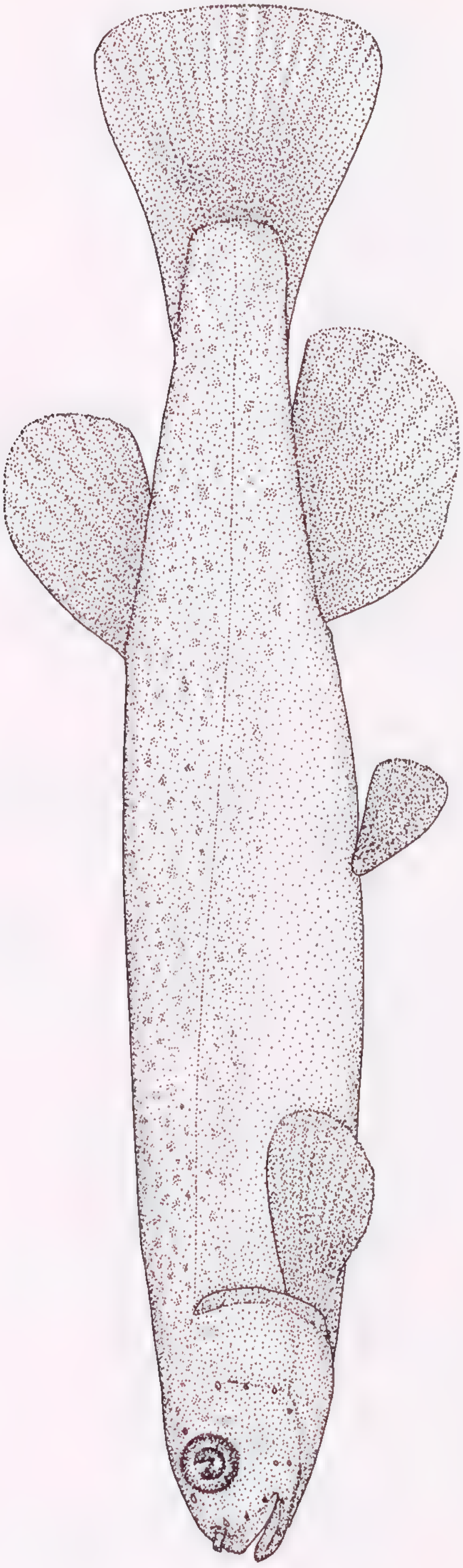

Fig. 24. *Galaxias parvus* Frankenberg; Lake Pedder, Tas., 63 mm T.L.

Fins well developed, somewhat fleshy-based, dorsal and anal fins short-based but high and rounded, the fins extending back moderately behind fin bases; anal fin origin set back a little behind dorsal origin. There is a low, ray-less, fleshy ridge in front of the dorsal fin. Pectoral fins small and fan-shaped, especially in small specimens, pedunculate, insertion moderately low laterally, lamina of fin vertical. Pelvic fins well developed, triangular, with outer rays longest, inserted a little behind mid-point of standard length. Caudal fin rounded, its depth about equal to body depth, caudal peduncle flanges strongly developed, especially ventrally.

Variation: meristic: See Table 10.
morphometric: see Table 11.

COLOUR: Live specimens have the back and sides greyish to yellowish-brown, becoming grey-green on the lower sides and whitish on the belly. The back and sides have numerous small and irregular dark grey-brown spots and blotches. There may be more or less conspicuous salmon-pink to gold colouration on the belly in front of the pelvic fins, especially in small fish. The operculum has a greenish iridescence. The fins are yellow-brown proximally becoming transparent distally.

Preserved specimens are dusky-brown on the back and sides with many small brown-black blotches and spots, irregular in size and spacing, the sides below the lateral line paler with melanophores forming lines along the myotomes. The belly is greyish-white to yellow. The fins are dusky at the bases but otherwise transparent.

SIZE: Andrews (1976) reported that *G. parvus* reaches a length of 75 mm S.L., or about 86 mm T.L. Fish larger than about 70 mm T.L. are uncommon.

HABITAT: *G. parvus* was collected from swamps, still pools, and backwaters, mainly by sweeping a dip net through vegetation at the margins of pools. Juveniles were collected in open, shallow water on the edge of Lake Pedder, together with adults and juveniles of *G. pedderensis*.

LIFE HISTORY: Some female *G. parvus* collected in February-March had immature gonads, others had ovaries showing marked development, although they were far from maturity. Andrews (1976) found juveniles 25-35 mm S.L. to be "abundant around the edges of Lake Pedder during early January" and he concluded that "it would appear that spawning takes place following the winter rains when surface water is abundant". The entire life cycle is spent in fresh water.

DISTRIBUTION: *G. parvus* is found only in the uplands of south-western Tasmania, in headwaters of the Gordon River, flowing north-west, and the Huon River, flowing south-east from a relatively small common divide (Fig. 23).

### **Galaxias maculatus** (Jenyns)

Fig. 26

*Mesites maculatus* Jenyns, 1842: 119 (holotype: BMNH 1917.7.14:6, not seen; paratypes: (3) BMNH 1917.7.14:7-9, not seen; type locality: Freshwater brook, Hardy Peninsula, Tierra del Fuego — senior synonym, Stokell (1966), first revisor).

*Mesites attenuatus* Jenyns, 1842: 121 (holotype: BMNH 1917.7.14:11, not seen; type locality: freshwater, Bay of Islands, New Zealand).

*Galaxias attenuatus* — Valenciennes, in Cuvier and Valenciennes, 1846: 348; Kner, 1865: 320; Günther, 1866: 210; Krefft, 1869: 103; 1871: 84; Castelnau, 1872: 176; Klunzinger, 1880: 412; Macleay, 1881: 46; 1882: 230; Seal et al. 1883: lvi:

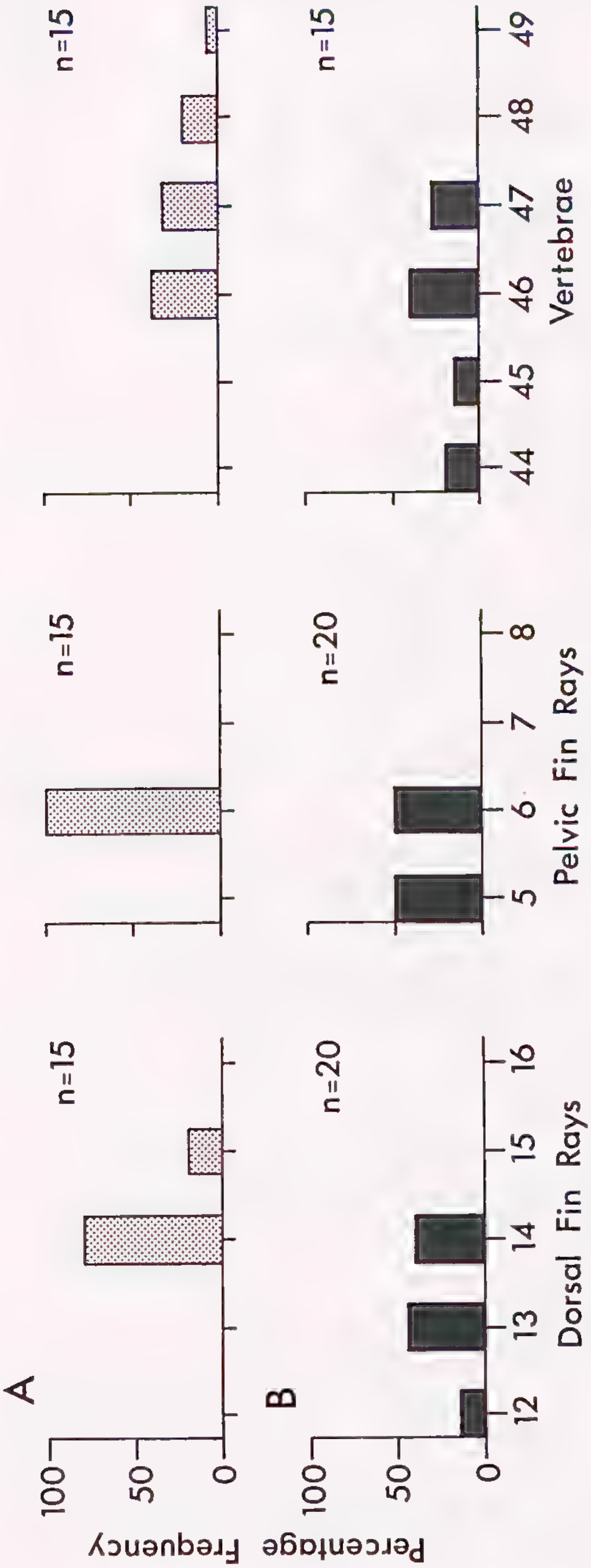

Fig. 25. Variation in the number of dorsal fin rays, pelvic fin rays and vertebrae in *Galaxias parvus*; **a.** Huon River; **b.** Serpentine River.

Table 10. Meristic variation in *Galaxias cleaveri* and *G. parvus*.

| | | *G. cleaveri* | | | | *G. parvus* | |
|---|---|---|---|---|---|---|---|
| | | Launceston, Tas. | West Coast Pieman-Queenstown, Tas. | Port Davey, Tas. | Dover, Tas. | Serpentine R., Tas. | Huon R., Tas. |
| Dorsal rays — segmented | 9 | | 3 | 3 | 1 | 6 | 5 |
| | 10 | 1 | 4 | 1 | 6 | 3 | 7 |
| | 11 | 2 | 3 | 2 | 1 | | |
| total | 10 | | | | | 3 | |
| | 11 | | 2 | 3 | 1 | 9 | |
| | 12 | 1 | 4 | 1 | 6 | 8 | 12 |
| | 13 | 2 | 4 | 1 | 1 | | 3 |
| | 14 | | | 1 | | | |
| Anal rays — segmented | 10 | | | 1 | | 3 | |
| | 11 | 1 | 7 | 1 | 4 | 5 | 8 |
| | 12 | 2 | 2 | 3 | 4 | 1 | 4 |
| | 13 | | 1 | 1 | | | |
| total | 11 | | | | | 2 | |
| | 12 | | | | | 5 | |
| | 13 | 1 | 4 | 2 | 3 | 6 | 5 |
| | 14 | 2 | 5 | 3 | 5 | 5 | 7 |
| | 15 | | 1 | 1 | | 2 | 3 |
| Caudal rays | 14 | | | | | 2 | |
| | 15 | | | | | 8 | |
| | 16 | 3 | 9 | 6 | 8 | 9 | 14 |
| | 17 | | 1 | | | 1 | 1 |
| Pectoral rays | 11 | | | | | 1 | |
| | 12 | | | | | 8 | 7 |
| | 13 | 1 | 2 | 5 | 6 | 8 | 7 |
| | 14 | 2 | 7 | 1 | 2 | 3 | 1 |
| Pelvic rays | 5 | | | | | 10 | |
| | 6 | | | 1 | | 10 | 15 |
| | 7 | 3 | 10 | 5 | 8 | | |
| Gill rakers | 9 | | 2 | | | 1 | |
| | 10 | | 1 | | 1 | 4 | 3 |
| | 11 | | 4 | 1 | 1 | 3 | 5 |
| | 12 | 2 | 3 | 5 | 5 | 1 | 3 |
| | 13 | 1 | | 1 | | | 1 |
| Vertebrae | 44 | | | | | 3 | |
| | 45 | | | | | 2 | |
| | 46 | | | | | 6 | 6 |
| | 47 | | | | | 4 | 5 |
| | 48 | | | | | | 3 |
| | 49 | | | | | | 1 |
| | 56 | 1 | 2 | | 1 | | |
| | 57 | 1 | 12 | 1 | 5 | | |
| | 58 | | 9 | 4 | 4 | | |
| | 59 | | 4 | 1 | 1 | | |
| | 60 | | 1 | | 1 | | |

Table 11. Morphometric variation in *Galaxias cleaveri* and *G. parvus*. Figures are given as percentages of denominators in ratios.

| | *G. cleaveri* | | | | | | | | | | *G. parvus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Launceston, Tas. | West Coast Pieman-Queenstown, Tas. | | Port Davey, Tas. | | Dover, Tas. | | All data | | | | | | |
| | Mean | Mean | S.D. | Mean | S.D. | Mean | S.D. | Min. | Mean | Max. | Min. | Mean | Max. | S.D. |
| S.L./T.L. | 86.70 | 88.60 | 1.24 | 88.57 | 2.34 | 88.75 | 1.12 | 84.2 | 88.42 | 91.1 | 85.2 | 87.22 | 89.0 | 0.82 |
| B.D.V./S.L. | 12.23 | 11.55 | 1.28 | 11.07 | 0.99 | 11.61 | 1.25 | 10.0 | 11.54 | 14.2 | 11.6 | 13.34 | 15.4 | 0.83 |
| L.C.P./S.L. | 13.70 | 12.37 | 0.34 | 11.48 | 0.15 | 12.06 | 0.76 | 11.0 | 12.23 | 15.0 | 14.0 | 16.09 | 18.7 | 1.31 |
| D.C.P./L.C.P. | 71.00 | 69.71 | 6.75 | 71.92 | 5.37 | 75.55 | 8.06 | 63.6 | 72.07 | 92.3 | 48.3 | 55.30 | 63.4 | 5.14 |
| Pre D./S.L. | 71.07 | 72.57 | 1.21 | 74.28 | 0.55 | 72.80 | 1.48 | 70.6 | 72,85 | 76.1 | 66.3 | 68.31 | 70.5 | 1.33 |
| Pre D./Pre A. | 94.57 | 94.60 | 2.03 | 97.02 | 0.58 | 94.23 | 1.07 | 91.9 | 95.02 | 97.9 | 91.0 | 95.22 | 98.4 | 2.09 |
| L.D.B./S.L. | 13.30 | 10.79 | 1.02 | 10.77 | 0.55 | 10.86 | 1.02 | 9.0 | 11.08 | 13.6 | 9.9 | 11.31 | 13.0 | 0.90 |
| M.L.D./L.D.B. | 147.60 | 163.08 | 7.19 | 162.73 | 11.29 | 159.18 | 6.95 | 144.0 | 160.10 | 175.0 | 145.0 | 162.73 | 185.7 | 11.81 |
| L.A.B./S.L. | 14.17 | 12.14 | 0.95 | 11.95 | 0.78 | 12.96 | 0.79 | 10.7 | 12.57 | 14.6 | 11.5 | 13.19 | 14.7 | 0.93 |
| M.L.A./L.A.B. | 140.83 | 147.53 | 7.50 | 151.85 | 10.93 | 140.54 | 4.81 | 133.3 | 145.67 | 170.0 | 123.3 | 144.93 | 172.2 | 11.11 |
| Pec./Pec.Pel. | 45.13 | 34.01 | 3.41 | 37.68 | 3.14 | 37.06 | 3.81 | 27.2 | 36.96 | 51.0 | 37.0 | 42.98 | 50.0 | 3.65 |
| Pel./Pel.An. | 48.00 | 38.88 | 6.93 | 39.42 | 4.34 | 42.05 | 4.37 | 27.3 | 40.95 | 52.9 | 51.0 | 61.15 | 72.0 | 6.30 |
| Pre.Pel/S.L. | 51.97 | 52.82 | 1.75 | 52.25 | 1.14 | 53.29 | 1.28 | 49.7 | 52.74 | 55.6 | 51.0 | 53.46 | 55.5 | 1.23 |
| Pec.Pel/S.L. | 31.40 | 33.96 | 1.65 | 33.02 | 1.38 | 33.40 | 0.83 | 30.1 | 33.30 | 36.6 | 28.4 | 31.80 | 36.5 | 1.78 |
| Pel.An./S.L. | 22.93 | 24.42 | 1.01 | 24.68 | 0.89 | 23.74 | 1.17 | 21.5 | 24.11 | 26.6 | 16.1 | 18.45 | 20.4 | 1.15 |
| H.L./S.L. | 22.33 | 20.11 | 1.18 | 19.88 | 0.67 | 20:95 | 1.13 | 18.7 | 20.55 | 23.3 | 22.3 | 23.39 | 24.7 | 0.66 |
| H.W./H.L. | 59.60 | 56,51 | 4.80 | 60.27 | 3.10 | 59.14 | 4.81 | 50.0 | 58.47 | 65.5 | 50.0 | 54.90 | 62.1 | 4.03 |
| H.D./H.L. | 55.53 | 54.08 | 3.36 | 54.27 | 2.88 | 53.09 | 3.98 | 48.1 | 53.99 | 62.1 | 52.2 | 57.10 | 62.1 | 2.99 |
| Sn.L./H.L. | 30.67 | 28.03 | 2.14 | 27.48 | 0.99 | 27.30 | 1.90 | 23.7 | 27.98 | 31.6 | 25.0 | 27.93 | 31.0 | 1.94 |
| P.O.H.L./H.L. | 60.43 | 61.36 | 3.42 | 60.92 | 1.88 | 60.46 | 2.68 | 55.1 | 60.89 | 65.7 | 47.7 | 52.90 | 59.0 | 2.97 |
| J.O.W./H.L. | 40.27 | 37.70 | 2.79 | 37.75 | 2.15 | 35.35 | 1.66 | 31.6 | 37.30 | 41.3 | 28.3 | 36.66 | 44.2 | 3.87 |
| D.E./H.L. | 16.20 | 15.67 | 1.48 | 14.75 | 1.55 | 16.41 | 1.66 | 12.5 | 15.74 | 18.8 | 19.4 | 22.84 | 26.3 | 1.98 |
| L.U.J./H.L. | 34.63 | 33.89 | 1.62 | 34.67 | 1.50 | 33.89 | 2.00 | 30.2 | 34.14 | 37.5 | 32.4 | 34.24 | 37.9 | 1.62 |
| L.L.J./H.L. | 33.93 | 32.60 | 2.04 | 34.20 | 0.86 | 33.29 | 1.46 | 29.7 | 33.31 | 35.9 | 29.2 | 32.30 | 36.1 | 1.84 |
| W.G./H.L. | 32.27 | 33.30 | 2.40 | 37.10 | 3.02 | 35.39 | 1.61 | 30.0 | 34.65 | 37.9 | 29.7 | 33.19 | 36.4 | 2.01 |
| N | 3 | 10 | | 6 | | 8 | | | 27 | | | 21 | | |

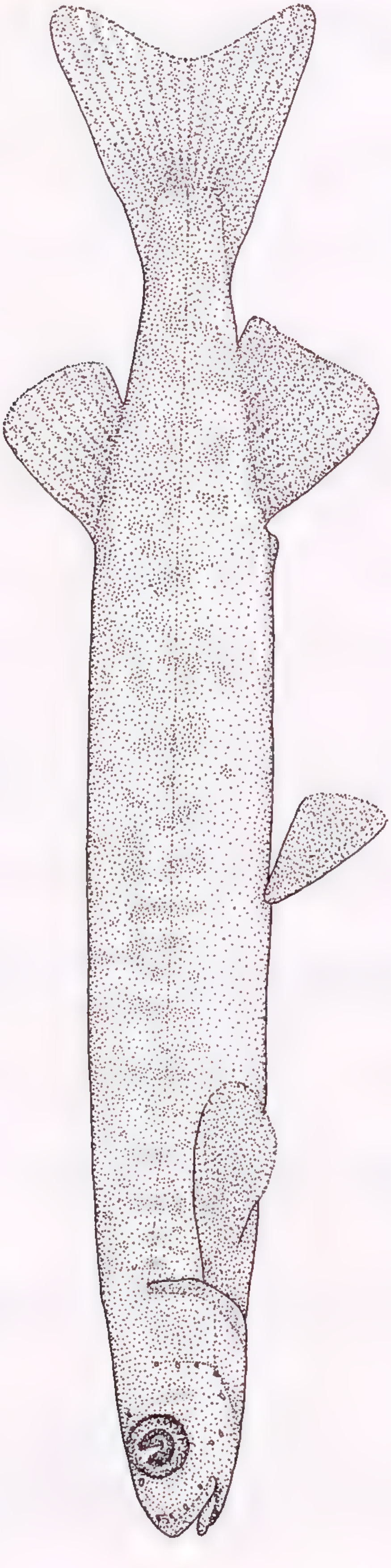

Fig. 26. *Galaxias maculatus* (Jenyns); Gulpa Creek, N.S.W., 89 mm L.C.F.

Tenison-Woods, 1883: 14; Johnston, 1883: 118; Lucas, 1890: 35; Ogilby, 1896: 64; Anderson, 1900: 25; Spencer, 1900: 161; Zietz, 1902: 267; Johnston, 1902: 55; Boulenger, 1903: 84; Regan, 1905: 368; Zietz, 1908: 297; McCulloch, 1914: 328; Gale, 1915: 16; Meek, 1916: 147; McCulloch, 1915: 47; Phillips, 1919: 211; Waite, 1921: 40; McCulloch, 1921: 28; 1922: 18; Lord, 1923: 63; Lord and Scott, 1924: 33; Waite, 1924: 483; McCulloch, 1925: 687; Nettlebeck, 1926: 65; Paradice, 1926: 43; Lord, 1927: 12; McCulloch, 1927: 18; Hale, 1928: 25; Waite, 1928: 4; Marshall, 1928: 189; Whitley, 1928: 59; McCulloch, 1929: 47; Mahony, 1935: 73; Scott, 1936: 113; Mack, 1936: 99; Johnston and Mawson, 1940: 350; Mack, 1941: 108; Anon. 1944: 2; Johnston and Mawson, 1944: 65; Crowcroft, 1945: 65; Stokell, 1945: 124; Butcher, 1945: 24; 1946; 9; 1947: 12; Butcher and Thompson, 1947: 15; Fairbridge, 1949: 73; Blackburn, 1950: 162; Stokell, 1950: 4; Bertin and Esteve, 1950: 3; Bleakley and Grant, 1954: 24; Stokell, 1953: 50; Manter, 1955: 67; Munro, 1957b: 15; Thompson, 1959: 306; Gentilli, 1961: 488; Scott, T., 1962: 67; Scott, E.O.G., 1963: 26; Stokell, 1964: 45; Lynch, 1965: 13; 1966: 13; Frankenberg, 1966a: 20; 1966b: 163; Breder and Rosen, 1966: 132; Frankenberg, 1967: 226; Lynch, 1967: 12; Lake, 1967: 193; Pollard, 1967: 9; Anon, 1968: 26; Lynch, 1968: 9; Bañarescu, 1968: 155; Lynch, 1969: 23; Green, 1969: 27; Scott, E.O.G. 1971a: 8; 1971b: 120; Green and McGarvie, 1971: 30; Munday and Green, 1972: 2; Grant, 1972: 405; McLean, 1974: 13; Scott, 1974: 254; Grant, 1975: 564; Baker, 1978: 822;

*Galaxias scriba* Valenciennes, in Cuvier and Valenciennes, 1846: 347 (holotype: MNHN A5217, not seen; type locality: Port Jackson and Port Darwin); Richardson, 1848: 76; Baird, 1861a: 269; 1861b: 207; Krefft, 1864: 182; Kner, 1865: 320: Günther, 1866: 212; Steindachner, 1866: 470; McCoy, 1867: 14; Macleay, 1881: 47; 1882: 232; Tenison-Woods, 1883: 22; Ogilby, 1886: 54; 1896; 68; Waite, 1904: 16; Stead, 1906: 50.

*Galaxias krefftii* Günther, 1866: 211 (syntypes: (1) BMNH 1861.3.25:3, not seen; (1) AMS I.7437, seen, sent to AMS by Regan; type locality "Sydney" and "Murray River"); Krefft, 1871: 84; Macleay, 1881: 47; 1882: 231; Tenison-Woods, 1883: 22; Ogilby 1886: 54; 1896: 69; Waite, 1904: 16; Whitley, 1956a: 34.

*Galaxias punctatus* Günther, 1866: 212 (holotype: BMNH 1864.7.22:49, not seen; type locality: "Eastern Creek, Australia"); Krefft, 1871: 84; Macleay, 1881: 47; 1882: 234; Tenison-Woods, 1883: 22; Ogilby, 1886: 54; 1896: 69; Waite, 1904: 16.

*Galaxias pseudoscriba* McCoy, 1867: 14 (holotype: unknown; type locality: Yarra River, Victoria).

*Galaxias waterhousei* Krefft, 1867: 943 (syntypes: (5) AMS I. 11384-8, seen; type locality: Creeks in South Australia); Macleay, 1881: 47; 1882: 253.

*Galaxias forsteri* — Kner, 1867: 320 (*partim;* non *Galaxias forsteri* Valenciennes, in Cuvier and Valenciennes, 1846: 532; syn *Galaxias argenteus* (Gmelin, 1789) New Zealand, see McDowall 1970a).

*Galaxias cylindricus* Castelnau, 1872: 177 (holotype: unknown; type locality: Lower Yarra River); Macleay, 1881: 47; 1882: 235; Lucas, 1890: 35; Ogilby, 1896: 69.

*Galaxias delicatulus* Castelnau, 1872: 178 (holotype: unknown; type locality: Yarra River); Macleay, 1881: 47; 1882: 235; Spencer, 1888: 164; Lucas, 1890: 35; Ogilby, 1896: 69.

*Galaxias versicolor* Castelnau, 1872: 176 (holotype: unknown; type locality: "in marsh near St. Kilda, Victoria"); Macleay, 1881: 47; 1882: 235; Lucas, 1890: 36; Ogilby, 1896: 69; McCulloch, 1921: 47.

*Galaxias amoenus* Castelnau, 1872: 178 (holotype: unknown; type locality: Yarra River); Macleay, 1881: 47; 1882: 235; Lucas, 1890: 36; Ogilby, 1896: 69; McCulloch, 1929: 49; Whitley, 1956a: 34.

*Galaxias obtusus* Klunzinger, 1872: 41 (lectotype: AMS I.19743-001, formerly SMNS 1599, seen; paralectotype (1) SMNS 1599, seen; type locality: Yarra Lagoon): Macleay, 1881: 47; Lucas, 1890: 36.

*Galaxias nebulosa* Macleay, 1881: 234 (syntypes: (5) formerly MMS F.83A, now AMS I.16260-001; type locality: Long Bay, near Sydney); Tenison-Woods, 1883: 22; Ogilby, 1886: 55; 1896: 69; Stanbury, 1969: 205.

*Austrocobitis attenuatus* — Ogilby, 1900: 158; 1908: 6; Iredale and Whitley, 1932: 96; Whitley, 1935: 44; Walford, 1941: 234; Whitley, 1956a: 33; 1956b: 39; 1957a: 6; 1957b: 9; 1960: 28; 1962: 52.

*Galaxeus attenuatus* — Noetling, 1911: 253 (mis-spelling of *Galaxias*).

*Galaxias attenuata* — Gray, 1930: 23.

*Austrocobitis attenuatus scriba* — Whitley, 1933: 61; 1964: 35; Scott, 1966: 246.

*Galaxias (Galaxias) attenuatus* — Scott, 1936: 90; 1938: 111; 1941: 59; 1942: 56.

*Galaxias parrishi* Stokell, 1964: 46 (holotype: NMVM A.242, seen; paratype: (1) NMW 3961, seen; type locality; Lake Bullen Merri, Victoria); Pollard, 1971b: 127; Dixon, 1972: 121.

*Galaxias maculatus ignotus* Stokell, 1966: 78 (holotype: none deposited; type locality: not formally designated although "Tasmania").

*Galaxias maculatus* — McDowall, 1967a; 841; 1969: 804; Lynch, 1970: 15; McDowall, 1970a: 378; 1970b: 18; 1971: 49; Lake, 1971: 20; Lynch, 1971: 13; Pollard, 1971a: 91; 1971b: 125; 1971c: 26: 1972a: 17; 1972b: 39; McDowall, 1972: 335; Lynch, 1972: 12; Andrews, 1973: 103; Pollard, 1973: 281; Timms, 1973: 13; Campos, 1973: 301; Chessman and Williams, 1974: 168; Scott, et al., 1974: 76; Rosen, 1974: 315; Pollard, 1974: 105; Frankenberg, 1974: 85; Grant, 1975: 564; Chessman and Williams, 1975: 135; Thompson, 1974: 150; Frankenberg, 1974: 121; Cassidy and Lake, 1975: 27; Nelson, 1976: 102; Glover and King, 1976: 188; Andrews, 1976: 305; Lynch, 1977: 13; Cadwallader, 1977: 22; Lake and Bennison, 1977: 59; McDowall 1978c: 69; 1978d: 97; Lake, 1978: 23; Williams, 1978: 29; Bishop and Bell, 1978: 545.

*Galaxias attenuatus scriba* — Scott, 1968: 1.

*Galaxias maculatus scriba* — Frankenberg, 1971: 95.

Additional synonyms from New Zealand and South America (from McDowall, 1971, 1972):

*Mesites alpinus* Jenyns, 1842, (South America).

*Galaxias maculatus attenuatus* (Jenyns, 1842) (New Zealand).

*Galaxias minutus* Philippi, 1858 (South America).

*Galaxias punctulatus* Philippi, 1858 (South America).

*Mesites gracillimus* Canestrini, 1864 (South America).

*Galaxias forsteri* Kner, 1867 (South America).

*Galaxias coppingeri* Günther, 1881 (South America).

*Galaxias variegatus* Lahille, 1923 — non *Stomias variegatus* Lesson, 1830, (South America).

*Galaxias titcombi* Eigenmann, 1928 (partim — South America).

*Galaxias usitatus* McDowall, 1967c (New Zealand).

TAXONOMY: The taxonomy of *G. maculatus* has been the subject of prolonged, extensive, and frequent discussion. Some of this discussion has centred upon the taxonomy of isolated populations in Australia, New Zealand and South America (Stokell, 1966: McDowall, 1967a, 1972; Scott, 1968), and some concerns the relationship of landlocked populations to diadromous ones (Stokell, 1964; McDowall, 1967a, 1972, 1976b; Pollard, 1971a; Campos, 1974). It is our view that populations of diadromous *G. maculatus* in mainland Australia, Tasmania, Lord Howe Island, New Zealand, the Chatham Islands, Chile, Argentina, Tierra del Fuego, and Falkland Islands, represent the single species *G. maculatus* (Jenyns) (McDowall, 1972). The name *G. maculatus* (Jenyns, 1842) has priority over *G. attenuatus* (Jenyns, 1842) (Stokell, 1966, first revisor). This view is held by most workers (see synonymy), although Scott (1968, 1971b, 1974) continues to use the name *G. attenuatus*.

Stokell (1966) recognised three subspecies, one each in Australia (*G. maculatus ignotus* Stokell), New Zealand (*G. maculatus attenuatus* (Jenyns)) and South America (*G. maculatus maculatus* (Jenyns)), but subsequent examination of larger samples has shown that differences recognised by Stokell are due to the very limited size of the samples he examined (McDowall, 1967a). Populations of this species, separated by wide expanses of ocean, are indistinguishable by standard morphometric and meristic characters. Campos (1972) examined karyotypes of this species from Australia and Chile, and found them identical, but Merriless (1975) found that New Zealand material he studied had differences in the number of chromosome arms although the chromosome number was the same. Merriless did not suggest taxonomic separation on this basis. If subspecies should be recognised for Australian populations, the name *ignotus* Stokell is a junior synonym of many others, of which *scriba* Valenciennes, in Cuvier and Valenciennes (1846) is the oldest.

The question of the status of landlocked populations is complex. *G. alpinus* (Jenyns, 1842), described from Peninsula Hardy, Tierra del Fuego, probably came from a lacustrine population (McDowall, 1971). Stokell (1964) described *G. parrishi* from Lake Bullen Merri, Victoria, and McDowall (1967c) described two species (*G. gracilis* and *G. usitatus*) from New Zealand lakes. The discovery of many more landlocked populations in Australia, New Zealand, and South America prompted a re-evaluation of the taxonomic status of these populations (McDowall, 1972), with the outcome that *G. alpinus, G. parrishi* and *G. usitatus* were treated as synonyms and no more than landlocked races of *G. maculatus*. Pollard (1971a) agreed with this view but Campos (1974) did not. He studied populations of *G. maculatus* in the Rio Calle Calle and its tributaries in central-southern Chile, and suggested that freshwater-limited populations in upper reaches of this river system should be recognised as a distinct species, for which he used the name *G. alpinus* (Jenyns). Campos based his view primarily on differences in vertebral counts which he assumed to indicate reproductive isolation. That there are serious practical and theoretical problems involved in the use of *G. alpinus* for the Rio Calle Calle populations was pointed out by McDowall (1976b). Following Campos' criteria, Australian and New Zealand landlocked populations should also be included in *G. alpinus,* but Campos does not discuss the implications of this. The position adopted here is that all freshwater-limited populations of *G. maculatus* in Australia should be "regarded as no more than isolated "ecological race(s)" of *G. maculatus* (Pollard, 1971b: 125, writing of the population in Lake Modewarre, Victoria).

Landlocked populations in Australia are known from Lakes Colac and Bullen Merri (Stokell, 1964), Modewarre (Pollard, 1971a), Corangamite, Rosine, Gnarpurt (Chessman and Williams, 1974), Wurdibolac, Purrumbete, Windimere, and others. These populations differ from diadromous *G. maculatus* in characters discussed at length by McDowall (1972), primarily in the marked reduction in vertebral number (low 60's in diadromous populations and mid 50's in lacustrine ones), and a variable increase in the number (Table 12) and length of the gill rakers.

Populations of *G. maculatus* are reported here for the first time from Western Australia (much material of this species in the collections of the Western Australian Museum has been misidentified as *G. truttaceus*). *G. maculatus* occurs as apparently freshwater-limited populations in rivers draining to the south coast of Western Australia as far west as the Goodja River, at which point its range overlaps the eastern fringes of *G. occidentalis* (Fig. 28). In general form and appearance the Western Australian populations of *G. maculatus* are typical of the species except that pigmentation is usually weakly developed. Like freshwater populations elsewhere, they have somewhat longer heads than diadromous ones (Table 13), slightly lower dorsal and anal fin ray counts but counts comparable with lake populations in Victoria (Table 12), Vertebral counts are reduced, in one population to a mean of 51.48 (Fitzgerald River), but there is broad overlap between Western Australian and Victorian populations (Table 12). For this reason it seems that taxonomic recognition of the Western Australian populations in spite of the great geographical isolation from other populations, is not justified.

There seems little evidence of clinal variation in the characters of diadromous populations studied. McDowall (1972) showed that there is evidence for a rise in vertebral number in more southern populations of *G. maculatus;* our data support this for Australian populations, although the differences are small (Table 12).

DIAGNOSIS: Characterised by slender form, small pectoral and pelvic fins, forked caudal fin, the absence of pyloric caeca on stomach and of lateral canine teeth in jaws, and high anal fin ray count. It resembles *G. rostratus* in these characters, but has a smaller mouth that only just reaches the front of the eyes. *G. rostratus* is found only in the inland Murray-Darling River system and is sympatric with *G. maculatus* only at the mouth of this river system.

Differs from *G. occidentalis* in lacking lateral canine teeth and fangs at the mandibular symphysis. The mouth is smaller in *G. maculatus,* the jaws equal (lower protrudes in *G. occidentalis)* and there are more anal fin rays. *G. maculatus* lacks the distinctive dark bars on the sides of *G. occidentalis.*

DESCRIPTION: A small to moderate-sized, elongate, and slender-bodied species, somewhat compressed along the whole trunk, belly little to moderately deepened, trunk profiles slightly to moderately and evenly arched; body deepest at about pelvic fins. Trunk tapers to a slender caudal peduncle that is longer than deep. Head short to moderate in length, about as deep as broad, cheeks not broadening below eyes. Snout bluntly pointed. Mouth slightly oblique, small, extending to below about anterior eye margins, jaws subequal. Eyes moderate to large, towards upper head profile, interorbital flat to slightly convex. Jaws with lateral canines. Mesopterygoidal teeth well developed; gill rakers of moderate length and quite stout (Fig. 43). No pyloric caeca or occasionally blunt shoulders at pyloric end of intestine (Fig. 45). Laterosensory pores on head as in Fig. 47

Fins small, not fleshy at bases. Dorsal fin short-based, fin extending somewhat behind base; anal fin origin below dorsal origin, much longer based and lower than dorsal, hindmost rays much shorter than anterior ones, fin extending little behind fin base. Pectoral fins small and paddle-shaped, insertion distinctly lateral; pelvic-anal interval long, pelvic fins very short, inserted at about mid-point of standard length. Caudal fin with a distinct but shallow fork, fin tips rounded, fin depth about equal to body depth peduncle flanges weak.

Variation: meristic: see Table 12.
morphometric: see Table 13.

COLOUR: When alive a translucent grey-olive to amber, with the back and upper sides covered by irregular and variable darker greenish-grey spots, blotches or bands. Colouration tends to be paler and the pattern indistinct in smaller fish, becoming bolder with growth. Sometimes little pattern. Lower sides, gill covers and eyes bright silvery. Fins largely unpigmented, with a few melanophores along rays.

In preservative a pale creamish-white to grey, the back and sides covered with darker greenish-grey to dark grey markings; these fail latero-ventrally and ventrally where the trunk is whitish. Colour darkens to brown after long storage in alcohol.

SIZE: *G. maculatus* is known to grow to at least 190 mm. Diadromous populations commonly contain fish reaching about 100 mm, and fish much larger than this are exceptions. Landlocked populations vary greatly in maximum size but Pollard (1971a) reported a mean L.C.F. of 112 mm (range 81-135 mm) for the Lake Modewarre population.

HABITAT: *G. maculatus* is found in a wide variety of habitats, but is most commonly found and is most abundant in still or gently flowing waters, mostly in streams, rivers and lakes at low altitudes and short distances from the sea. Chessman and Williams (1974, 1975) have shown that this species has a very wide range of salinity tolerances. It occurs naturally in waters with salinities up to 49°/00 and experiments showed that with acclimation the $LD_{50}$ value was 62°/00; the $LD_{50}$ value for direct transfer from water of 30°/00 was 45°/00. Euryhalinity in *G. maculatus* enables it to inhabit some of the many saline lakes of Victoria.

LIFE HISTORY: Because of its economic importance in New Zealand the natural history of *G. maculatus* has been much studied there (see McDowall, 1968b: McDowall and Eldon, 1981). Less work has been done on Australian and South American populations (see however, Pollard, 1971a, b, c, 1972a, b, 1973, 1974, Campos, 1972, 1974).

Reproduction in diadromous stocks of *G. maculatus* in New Zealand has been shown to be as follows: during autumn, shoals of mature to ripe adults migrate downstream into estuaries at about the time of the full and new moons (spring tides). The fish swim amongst dense terrestrial vegetation inundated at the high spring tide and deposit their eggs there. For the following two weeks the eggs develop out of water in the humid atmosphere around the vegetation, and they hatch when a second series of spring tides again inundates the vegetation. The newly hatched larvae are washed out to sea (Phillipps 1924; Hefford, 1931a, b, 1932; Burnet, 1965; Benzie, 1968b; McDowall, 1968b). It is generally assumed that reproduction of the species in Australia is comparable (Phillipps, 1919; Whitley, 1935; Pollard, 1971a; Andrews, 1976).

The spring upstream migrations of the juveniles are better known in Australia (McCulloch, 1914; Scott, 1938; Blackburn, 1950) although the factors that affect these migrations remain unstudied. Apart from the studies of Pollard (1971a, b, c, 1972a, b,

Table 12. Meristic variation in *Galaxias maculatus* (Part 1).

| | | Hawkesbury R., N.S.W. | Tuross R., N.S.W. | Koo-wee-rup, Vic. | Wilsons Promontory, Vic. | Cardinia-Toomuc, Vic. | Otways, Vic. | Port Lincoln, S.A. | Port Macleay, S.A. | Kangaroo Is., S.A. | Flinders Is. | Northern Tasmania | Nelson Bay R., Tas. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dorsal rays — segmented | 7 | | | | | | | | | | | | |
| | 8 | | | | | | | | | | | | |
| | 9 | 5 | 2 | 2 | | | 2 | | | | | 1 | 2 |
| | 10 | 3 | 6 | 5 | | | 6 | | | | | 6 | 6 |
| | 11 | 1 | 2 | 3 | | | 2 | | | | | 3 | 2 |
| total | 9 | | | | | | | | | | | | |
| | 10 | 1 | | | | 2 | | | | | | | |
| | 11 | 1 | 2 | 1 | 1 | 7 | 14 | | | | | | 1 |
| | 12 | 4 | 6 | 3 | 3 | 13 | 16 | 4 | 5 | 9 | 3 | 6 | 2 |
| | 13 | 2 | 2 | 5 | 5 | 3 | 5 | 6 | 12 | 13 | 6 | 3 | 6 |
| | 14 | 1 | | 0 | 1 | | | | 1 | 3 | 1 | 1 | 1 |
| | 15 | | | 1 | | | | | | | | | |
| Anal rays — segmented | 10 | | | | | | | | | | | | |
| | 11 | | | | | | | | | | | | |
| | 12 | | | | | | | | | | | 1 | |
| | 13 | | | | | | | | | | | 0 | 1 |
| | 14 | 3 | 4 | 2 | | | 3 | | | | | 1 | 3 |
| | 15 | 6 | 3 | 5 | | | 4 | | | | | 7 | 4 |
| | 16 | | 3 | 3 | | | 3 | | | | | 0 | 1 |
| | 17 | | | | | | | | | | | 1 | 1 |
| | 18 | | | | | | | | | | | | |
| | 19 | | | | | | | | | | | | |
| total | 12 | | | | | | | | | | | | |
| | 13 | | | | | | | | | | | | |
| | 14 | | | | | | | | | | | | |
| | 15 | | | | 1 | | | | | | | 1 | |
| | 16 | 1 | 1 | 1 | 1 | 2 | 3 | 1 | | | | 0 | 1 |
| | 17 | 4 | 4 | 3 | 1 | 5 | 9 | 5 | 8 | 7 | 5 | 3 | 3 |
| | 18 | 4 | 3 | 4 | 6 | 13 | 18 | 3 | 7 | 13 | 4 | 5 | 4 |
| | 19 | | 2 | 2 | 1 | 5 | 4 | 1 | 3 | 4 | 1 | 0 | 1 |
| | 20 | | | | | | 1 | | | 1 | | 1 | 1 |
| | 21 | | | | | | | | | | | | |
| Pectoral rays | 10 | | | | | | | | | | | | |
| | 11 | | | 1 | | | 1 | | | | 1 | | |
| | 12 | 5 | 1 | 2 | 3 | 12 | 14 | 4 | 2 | 3 | 2 | 4 | 4 |
| | 13 | 4 | 5 | 7 | 7 | 13 | 17 | 4 | 7 | 16 | 7 | 4 | 6 |
| | 14 | | 4 | | | | 2 | 2 | 3 | 6 | | 2 | |
| | 15 | | | | | | 1 | | | | | | |

| *Southern Tasmania* | L. Windermere, N.S.W. | L. Corangamite, Vic. | L. Modewarre, Vic. | L. Bullen Merri, Vic. | L. Colac, Vic. | L. Purrumbete, Vic. | Wurdiboluc Res., Vic. | L. Bongbong, Vic. | Near L. Wangery, S.A. | Pallinup R., W.A. | Gairdner R., W.A. | Fitzgerald R., W.A. | Hamersley R., W.A. | Jerdacuttup R., W.A. | Dalyup R., W.A. | Shark L., W.A. | Sandy Ck, W.A. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | 4 | 1 |  | 1 |  |  |  |  |  |  | 1 |  |  |  |  |  |
|  |  | 4 | 4 | 14 | 10 |  |  |  |  |  |  | 1 |  |  | 7 |  |  |
| 3 | 6 | 2 | 9 | 6 | 6 |  |  |  |  |  | 4 | 7 |  |  | 7 |  |  |
| 12 | 2 |  | 6 |  | 2 |  |  |  |  |  | 6 | 1 |  |  | 1 |  |  |
| 15 | 2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  | 3 |  |  |  |  |  |  |  |  |  | 1 | 1 | 1 | 2 |  |  |
|  |  | 8 | 6 |  | 12 | 1 |  |  |  | 1 | 1 | 6 | 7 | 7 | 6 |  | 3 |
| 1 | 5 | 20 | 13 | 7 | 20 | 3 | 1 | 2 | 3 | 3 | 11 | 18 | 16 | 9 | 18 | 1 | 9 |
| 9 | 3 | 3 | 18 | 20 | 9 | 13 | 4 | 12 | 6 | 6 | 8 | 7 | 1 | 7 | 10 | 6 | 5 |
| 8 | 2 | 1 | 6 | 11 | 2 | 8 | 1 | 6 | 1 | 2 |  | 3 |  | 1 | 4 | 1 |  |
| 2 |  |  | 2 |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  | 1 |  |  | 1 |  |  |  |  |  |  | 1 |  |  | 1 |  |  |
|  |  | 7 | 6 |  | 7 |  |  |  |  |  |  | 3 |  |  | 4 |  |  |
|  | 4 | 1 | 6 | 6 | 10 |  |  |  |  |  |  | 5 |  |  | 7 |  |  |
| 5 | 1 |  | 7 | 12 | 1 |  |  |  |  |  | 7 | 0 |  |  | 2 |  |  |
| 9 | 4 |  | 1 | 2 |  |  |  |  |  |  | 3 | 1 |  |  | 1 |  |  |
| 3 | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  | 1 |  |  | 1 |  |  |
|  |  | 3 |  |  |  |  |  |  |  |  |  | 2 | 2 |  | 1 |  |  |
|  |  | 3 |  |  | 2 |  |  |  |  |  |  | 10 | 13 | 5 | 6 |  | 1 |
|  |  | 16 | 10 |  | 15 |  |  |  | 3 | 4 | 2 | 14 | 9 | 13 | 7 | 2 | 6 |
| 1 | 4 | 11 | 12 | 7 | 16 | 4 | 1 | 3 | 2 | 8 | 12 | 7 | 1 | 4 | 11 | 3 | 5 |
| 4 | 3 | 2 | 14 | 19 | 9 | 12 | 2 | 11 | 5 |  | 5 | 0 |  | 3 | 6 | 3 | 4 |
| 10 | 2 |  | 7 | 11 | 1 | 8 | 2 | 5 |  |  | 1 | 1 |  |  |  |  | 1 |
| 2 | 1 |  | 2 | 1 | 1 | 1 | 1 | 1 |  |  |  |  |  |  |  |  |  |
| 2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | — |  |
| 2 |  | 4 | 1 |  |  |  |  |  |  |  |  |  |  |  | 2 | — | 3 |
| 5 |  | 16 | 18 | 8 | 2 | 4 |  | 1 | 3 | 2 | 7 | 9 | 15 | 10 | 23 | — | 9 |
| 12 | 3 | 14 | 19 | 14 | 19 | 18 | 5 | 11 | 5 | 7 | 12 | 16 | 10 | 14 | 14 | — | 5 |
| 1 | 6 | 1 | 7 | 13 | 14 | 3 | 0 | 7 | 2 | 3 | 1 | 10 |  | 1 | 1 |  |  |
|  | 1 |  |  | 3 |  |  | 1 | 1 |  |  |  |  |  |  |  |  |  |

Table 12. Meristic variation in *Galaxias maculatus* (Part 2).

| | | Hawkesbury R., N.S.W. | Tuross R., N.S.W. | Koo-wee-rup, Vic. | Wilsons Promontory, Vic. | Cardinia-Toomuc, Vic. | Otways, Vic. | Port Lincoln, S.A. | Port Macleay, S.A. | Kangaroo Island, S.A. | Flinders Island | Northern Tasmania | Nelson Bay R., Tas. | Southern Tasmania | L. Windermere, N.S.W. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Caudal Rays | 14 | | | | | | | | | | | | | | |
| | 15 | 1 | | | | | | | | | | 1 | 1 | | |
| | 16 | 8 | 9 | 10 | 10 | 0 | | | | | | 9 | 9 | 20 | 9 |
| | 17 | | 1 | | | | | | | | | | | | 1 |
| Pelvic Rays | 6 | | | | | | | | | | | | | | 1 |
| | 7 | 9 | 10 | 10 | 8 | | | | | | | 10 | 10 | 18 | 9 |
| | 8 | | | | 2 | | | | | | | | | 2 | |
| Gill Rakers | 13 | | | | | | | | | | | 1 | | | |
| | 14 | | 1 | | 2 | | | | | | | 3 | | | |
| | 15 | 2 | 3 | 7 | 4 | | | | | | | 4 | 5 | | 1 |
| | 16 | 4 | 6 | 3 | 3 | | | | | | | 1 | 3 | | 5 |
| | 17 | 2 | | | 0 | | | | | | | | 1 | 1 | 4 |
| | 18 | 1 | | | 1 | | | | | | | | 1 | 2 | |
| | 19 | | | | | | | | | | | | | 3 | |
| | 20 | | | | | | | | | | | | | 3 | |
| | 21 | | | | | | | | | | | | | 1 | |
| Vertebrae | 50 | | | | | | | | | | | | | | |
| | 51 | | | | | | | | | | | | | | |
| | 52 | | | | | | | | | | | | | | |
| | 53 | | | | | | | | | | | | | | |
| | 54 | | | | | | | | | | | | | | |
| | 55 | | | | | | | | | | | | | | 5 |
| | 56 | | | | | | | | | | | | | | 10 |
| | 57 | 1* | | | 1 | 2 | | | | | | | | | 5 |
| | 58 | 2 | 3† | | 1 | 10 | 1 | | 1 | 1 | 1 | | 2 | | |
| | 59 | 6 | 8† | | 4 | 12 | 7 | 6 | 6 | 5 | 4 | | 11 | | |
| | 60 | 2 | 3 | | 3 | 1 | 8 | 4 | 10 | 13 | 2 | | 13 | | |
| | 61 | 1 | | | 1 | | 7 | | 2 | 5 | | | 10 | | |
| | 62 | | | | | | 2 | | 1 | 1 | | | 3 | | |

*Northern New South Wales
†Southern New South Wales

| L. Corangamite, Vic. | L. Modewarre, Vic. | L. Bullen Merri, Vic. | L. Colac, Vic. | L. Purrumbete, Vic. | Wurdiboluc Res., Vic. | L. Bongbong, Vic. | Near L. Wangary, S.A. | Pallinup R., W.A. | Gairdner R., W.A. | Fitzgerald R., W.A. | Hamersley R., W.A. | Jerdacuttup R., W.A. | Dalyup R., W.A. | Shark L., W.A. | Sandy Creek, W.A. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | | | |
| 1 | | | | | | | | | | | | | 1 | | |
| 9 | | 20 | 20 | | | | | | 10 | 8 | | | 14 | | |
| | | | | | | | | | | 2 | | | | | |
| | | | | | | | | | | | | | 1 | | |
| 10 | | 20 | 19 | | | | | | 10 | 10 | | | 14 | | |
| | | | 1 | | | | | | | | | | | | |
| 1 | | | | | | | | | | | | | 1 | | |
| 0 | 2 | | 1 | | | | | | | | | | 6 | | |
| 6 | 3 | 1 | 1 | | | | | | 2 | | | | 4 | | |
| 6 | 6 | 3 | 10 | | | | | | 2 | 4 | | | 2 | | |
| 5 | 4 | 4 | 8 | | | | | | 2 | 4 | | | 2 | | |
| 1 | 3 | 7 | | | | | | | 2 | 2 | | | | | |
| 1 | 2 | 4 | | | | | | | | | | | | | |
| | | 1 | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |
| | | | | | | | | | | 3 | | | | | |
| | | | | | | | | | 1 | 9 | 9 | 2 | | | |
| | | | 1 | | | | | | 2 | 11 | 6 | 11 | 1 | | |
| | | | 0 | | | | | 4 | 6 | 2 | 7 | 9 | 6 | | 2 |
| 9 | | 2 | 9 | 5 | | | | 5 | 1 | | 3 | 3 | 7 | 1 | 1 |
| 15 | 4 | 8 | 18 | 10 | | | | 3 | | | | | 10 | 4 | 8 |
| 1 | 5 | 22 | 12 | 8 | | | 1 | | | | | | 1 | 3 | 5 |
| | 19 | 13 | 3 | 2 | | 8 | 4 | | | | | | | | 1 |
| | 11 | 1 | 0 | | 1 | 5 | 4 | | | | | | | | |
| | 4 | | 2 | | 2 | 6 | 1 | | | | | | | | |
| | 1 | | 1 | | 3 | 1 | | | | | | | | | |
| | 1 | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |

Table 13. Morphometric variation in *Galaxias maculatus*.
Figures are given as percentage of denominators in ratios.

| | | S.L./T.L. | B.D.V./S.L. | L.C.P./S.L. | D.C.P./L.C.P. | PreD./S.L. | PreD./Pre A. | L.D.B./S.L. | M.L.D./L.D.B. | L.A.B./S.L. | M.L.A./L.A.B. | Pec./Pec.Pel |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hawkesbury R. | Mean | 88.86 | 11.80 | 11.36 | 57.32 | 75.46 | 98.82 | 9.37 | 165.9 | 13.76 | 132.13 | 42.49 |
| N.S.W. | S.D. | 1.74 | 1.24 | 0.78 | 5.59 | 2.36 | 1.00 | 0.69 | 14.27 | 0.76 | 7.32 | 5.20 |
| Gulpa C.,Tuross R. | Mean | 90.11 | 11.35 | 11.31 | 57.46 | 75.42 | 99.85 | 9.13 | 157.01 | 14.11 | 123.52 | 39.77 |
| N.S.W. | S.D. | 0.91 | 0.77 | 0.67 | 4.72 | 1.13 | 1.29 | 0.87 | 14.33 | 0.63 | 4.51 | 2.63 |
| Koo-wee-rup | Mean | 89.67 | 11.78 | 10.81 | 61.99 | 75.95 | 99.49 | 9.35 | 159.80 | 14.56 | 122.70 | 40.68 |
| Vic. | S.D. | 0.62 | 0.54 | 0.76 | 6.94 | 1.94 | 1.38 | 0.63 | 8.47 | 0.61 | 5.13 | 3.19 |
| Otways | Mean | 89.43 | 11.82 | 10.84 | 61.96 | 74.75 | 99.13 | 8.93 | 160.84 | 13.71 | 125.94 | 41.13 |
| Vic. | S.D. | 0.65 | 1.13 | 0.91 | 6.37 | 2.07 | 0.9 | 0.51 | 11.08 | 0.88 | 6.44 | 4.23 |
| Northern | Mean | 89.16 | 11.83 | 11.57 | 57.24 | 74.63 | 99.21 | 10.17 | 149.59 | 14.86 | 120.92 | 45.09 |
| Tasmania | S.D. | 0.37 | 1.00 | 0.61 | 3.45 | 1.11 | 1.6 | 1.06 | 13.62 | 1.33 | 6.66 | 4.96 |
| Nelson Bay R. | Mean | 89.56 | 12.11 | 11.27 | 58.53 | 75.29 | 99.31 | 9.17 | 157.11 | 14.45 | 118.8 | 40.90 |
| Tasmania | S.D. | 0.61 | 0.64 | 0.65 | 5.02 | 0.92 | 1.16 | 0.79 | 13.33 | 0.46 | 2.06 | 2.77 |
| Southern | Mean | 88.97 | 13.30 | 11.81 | 62.77 | 76.02 | 99.51 | 10.49 | 151.04 | 14.25 | 129.49 | 44.80 |
| Tasmania | S.D. | 0.65 | 0.71 | 1.24 | 6.13 | 1.38 | 1.41 | 0.97 | 8.67 | 1.45 | 5.19 | 0.33 |
| L. Windermere | Mean | 88.49 | 9.87 | 11.09 | 53.14 | 75.06 | 99.70 | 9.09 | 146.90 | 13.32 | 126.02 | 46.93 |
| N.S.W. | S.D. | 0.69 | 0.62 | 1.15 | 5.58 | 1.00 | 1.21 | 0.99 | 15.61 | 1.36 | 11.08 | 3.47 |
| L. Corangamite | Mean | 88.68 | 11.48 | 12.17 | 57.46 | 73.66 | 98.58 | 7.73 | 174.79 | 11.77 | 130.46 | 43.23 |
| Vic. | S.D. | 0.80 | 1.07 | 1.48 | 5.54 | 3.55 | 1.56 | 0.52 | 12.25 | 1.37 | 6.73 | 3.32 |
| L. Modewarre | Mean | 88.95 | 11.85 | 11.40 | 58.66 | 75.77 | 98.77 | 9.24 | 164.67 | 12.45 | 129.58 | 41.43 |
| Vic. | S.D. | 0.90 | 0.75 | 0.53 | 2.72 | 1.07 | 1.47 | 0.40 | 11.86 | 1.38 | 6.73 | 3.16 |
| L. Bullen Merri | Mean | 87.36 | 11.49 | 11.34 | 60.08 | 76.14 | 99.28 | 9.16 | 160.08 | 12.45 | 129.29 | 48.60 |
| Vic. | S.D. | 1.29 | 0.86 | 0.59 | 6.12 | 1.10 | 1.35 | 0.71 | 11.09 | 0.88 | 6.43 | 3.31 |
| L. Colac | Mean | 88.58 | 11.85 | 12.13 | 57.36 | 75.44 | 98.71 | 8.89 | 161.50 | 13.29 | 126.62 | 43.88 |
| Vic. | S.D. | 0.53 | 0.61 | 0.34 | 4.37 | 0.95 | 0.50 | 0.52 | 8.24 | 0.46 | 9.52 | 1.66 |
| Fitzgerald R. | Mean | 88.27 | 11.40 | 11.36 | 60.61 | 75.87 | 98.00 | 8.83 | 175.40 | 12.35 | 139.46 | 48.10 |
| W.A. | S.D. | 0.53 | 1.00 | 0.87 | 7.33 | 1.43 | 1.09 | 0.96 | 14.24 | 0.96 | 5.66 | 3.21 |
| Gairdner R. | Mean | 89.13 | 11.72 | 10.38 | 62.86 | 75.96 | 98.62 | 8.97 | 157.65 | 13.86 | 126.05 | 41.24 |
| W.A. | S.D. | 0.90 | 0.43 | 0.55 | 4.50 | 0.92 | 1.07 | 0.60 | 10.78 | 0.72 | 6.00 | 2.00 |
| Dalyup R. | Mean | 88.46 | 11.91 | 12.27 | 64.44 | 74.33 | 98.15 | 9.11 | 161.21 | 12.68 | 136.77 | 43.46 |
| W.A. | S.D. | 1.18 | 0.92 | 0.11 | 5.49 | 1.25 | 1.70 | 1.02 | 12.40 | 1.14 | 6.17 | 2.53 |
| All data | Min | 85.3 | 8.7 | 9.4 | 41.9 | 67.3 | 95.2 | 6.6 | 127.3 | 9.1 | 112.8 | 33.8 |
| | Mean | 88.91 | 11.70 | 11.41 | 59.46 | 75.32 | 99.01 | 9.18 | 160.23 | 13.46 | 127.85 | 43.45 |
| | Max | 91.4 | 14.2 | 15.4 | 76.1 | 80.7 | 102.7 | 12.3 | 200.0 | 16.6 | 152.0 | 54.3 |

| Pel./Pel An | PrePel./S.L. | Pec.Pel./S.L. | Pel.An/S.L. | H.L./S.L. | H.W./H.L. | H.D./H.L. | Sn.L/H.L. | P.O.H.L./H.L. | I.O.W./H.L. | E.D./H.L. | L.U.J./H.L. | L.L.J./H.L. | W.G./H.L. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 40.67 | 48.82 | 29.52 | 27.81 | 20.10 | 49.53 | 52.69 | 28.83 | 53.09 | 38.04 | 22.79 | 33.82 | 32.17 | 28.87 |
| 4.90 | 1.31 | 1.73 | 1.55 | 1.29 | 2.17 | 3.33 | 2.25 | 1.94 | 3.20 | 2.34 | 2.03 | 2.03 | 2.74 |
| 38.62 | 49.22 | 29.84 | 28.11 | 20.23 | 50.28 | 53.05 | 30.11 | 52.21 | 38.12 | 21.98 | 34.08 | 32.59 | 28.52 |
| 2.60 | 0.98 | 1.49 | 1.48 | 0.53 | 3.58 | 2.59 | 1.58 | 1.19 | 1.42 | 1.90 | 1.70 | 1.80 | 2.80 |
| 41.40 | 50.10 | 29.95 | 28.16 | 20.41 | 52.36 | 53.48 | 30.02 | 52.94 | 37.98 | 21.87 | 32.69 | 30.14 | 31.40 |
| 3.01 | 1.32 | 1.10 | 1.00 | 0.63 | 1.76 | 2.32 | 1.29 | 2.12 | 2.12 | 1.67 | 1.20 | 2.18 | 2.30 |
| 40.55 | 49.58 | 30.33 | 28.35 | 19.79 | 52.99 | 55.98 | 30.67 | 53.49 | 37.40 | 24.13 | 35.83 | 34.05 | 29.64 |
| 3.82 | 1.36 | 1.62 | 2.06 | 0.65 | 3.34 | 2.12 | 1.84 | 2.68 | 2.03 | 2.83 | 2.68 | 2.51 | 1.95 |
| 40.83 | 47.72 | 27.48 | 27.60 | 20.76 | 50.69 | 52.42 | 28.34 | 51.50 | 36.68 | 22.96 | 33.30 | 31.29 | 28.36 |
| 2.60 | 0.99 | 1.46 | 1.48 | 0.76 | 3.24 | 2.49 | 2.04 | 1.64 | 1.29 | 2.34 | 1.60 | 1.73 | 3.17 |
| 41.56 | 49.56 | 29.98 | 27.39 | 20.89 | 52.87 | 55.37 | 28.48 | 52.82 | 39.37 | 22.00 | 33.69 | 30.72 | 29.39 |
| 2.54 | 0.76 | 1.14 | 1.07 | 0.64 | 1.82 | 1.38 | 0.85 | 2.32 | 1.69 | 2.05 | 1.70 | 2.08 | 1.50 |
| 44.00 | 49.74 | 28.89 | 26.99 | 21.64 | 51.08 | 48.84 | 27.77 | 52.00 | 37.26 | 23.28 | 32.20 | 31.40 | 30.33 |
| 5.35 | 1.17 | 0.92 | 0.97 | 1.00 | 2.19 | 3.14 | 0.92 | 1.86 | 1.86 | 1.15 | 1.29 | 0.98 | 2.44 |
| 46.52 | 50.91 | 27.85 | 24.57 | 23.88 | 45.59 | 45.43 | 28.52 | 53.92 | 32.53 | 25.54 | 35.63 | 35.37 | 24.86 |
| 3.80 | 1.84 | 1.79 | 1.06 | 0.81 | 1.56 | 1.85 | 2.41 | 2.49 | 1.38 | 2.70 | 2.16 | 2.07 | 1.84 |
| 42.74 | 49.99 | 27.93 | 26.16 | 22.16 | 48.54 | 51.58 | 28.03 | 53.27 | 35.08 | 22.81 | 32.14 | 31.59 | 28.47 |
| 2.94 | 2.37 | 1.84 | 2.09 | 1.50 | 2.03 | 2.62 | 1.00 | 2.04 | 2.56 | 3.08 | 1.39 | 1.29 | 1.91 |
| 39.20 | 49.36 | 30.01 | 27.73 | 20.44 | 50.35 | 51.20 | 29.07 | 55.34 | 39.20 | 19.76 | 33.03 | 31.74 | 29.47 |
| 3.45 | 1.17 | 1.42 | 1.26 | 0.84 | 2.97 | 1.51 | 1.40 | 2.38 | 1.80 | 1.98 | 1.87 | 1.50 | 1.23 |
| 44.27 | 50.83 | 27.78 | 25.45 | 23.32 | 47.11 | 48.58 | 26.43 | 54.56 | 34.12 | 20.81 | 31.61 | 30.67 | 27.04 |
| 3.27 | 1.06 | 1.20 | 0.79 | 1.10 | 2.04 | 2.40 | 1.62 | 2.26 | 0.97 | 2.08 | 2.87 | 1.49 | 0.67 |
| 44.91 | 49.85 | 29.10 | 26.75 | 21.01 | 49.65 | 51.87 | 28.10 | 53.12 | 35.67 | 22.23 | 33.15 | 31.52 | 28.20 |
| 3.38 | 0.72 | 0.88 | 1.21 | 0.49 | 1.69 | 2.88 | 1.49 | 0.99 | 2.41 | 1.49 | 1.70 | 1.50 | 1.69 |
| 44.16 | 51.36 | 28.17 | 27.15 | 23.28 | 50.53 | 51.20 | 28.48 | 55.85 | 34.19 | 20.07 | 36.78 | 35.28 | 29.10 |
| 4.59 | 1.29 | 1.78 | 1.90 | 0.62 | 2.97 | 3.26 | 2.05 | 1.57 | 1.88 | 1.48 | 1.94 | 2.40 | 2.98 |
| 39.85 | 51.05 | 29.37 | 27.65 | 22.61 | 46.12 | 49.36 | 29.01 | 53.51 | 34.37 | 20.42 | 35.88 | 35.66 | 28.15 |
| 2.33 | 1.01 | 1.19 | 1.13 | 0.60 | 1.90 | 2.30 | 1.03 | 2.18 | 0.92 | 2.00 | 1.74 | 2.08 | 2.96 |
| 44.57 | 50.55 | 29.51 | 25.83 | 22.27 | 50.14 | 52.80 | 28.46 | 56.11 | 35.02 | 22.46 | 35.19 | 35.05 | 28.17 |
| 3.65 | 1.07 | 1.30 | 1.04 | 0.56 | 3.17 | 3.04 | 2.09 | 2.51 | 2.65 | 2.17 | 2.61 | 2.88 | 2.61 |
| 31.7 | 45.6 | 24.2 | 21.8 | 17.7 | 42.1 | 42.3 | 22.8 | 47.8 | 30.8 | 16.7 | 28.4 | 27.7 | 22.0 |
| 42.26 | 49.91 | 29.05 | 27.05 | 21.52 | 48.86 | 51.57 | 28.69 | 53.58 | 36.34 | 22.21 | 33.93 | 32.62 | 28.70 |
| 53.3 | 53.3 | 32.9 | 31.5 | 25.3 | 61.5 | 59.1 | 33.3 | 60.5 | 43.2 | 30.8 | 40.0 | 40.0 | 38.3 |

1973, 1974), the natural history of *G. maculatus* in Australian fresh waters remains poorly known.

Pollard studied the landlocked population of *G. maculatus* in Lake Modewarre in Victoria. He showed that during the spring, spawning adults migrate upstream from the lake into flooding tributary streams and that they deposit their eggs on flooded stream-bank vegetation. The eggs are stranded when the flood subsides but survive and hatch when a subsequent flood re-immerses them two or more weeks later. The newly hatched larvae are washed downstream into the lake where they grow to maturity. Thus this landlocked population has reversed the direction of the spawning migration (upstream instead of downstream) and altered the season (spring instead of autumn), while retaining "terrestrial" deposition of the eggs and the essentially annual life cycle.

DISTRIBUTION: *G. maculatus* is found in Australia, Tasmania, Lord Howe Island, New Zealand, the Chatham Islands, Chile, Argentina, Tierra del Fuego and the Falkland Islands (McDowall, 1972; McDowall and Gosztonyi, 1975). It is one of the most widely distributed freshwater fishes. In Australia diadromous populations are known from coastal flowing streams and rivers east and south of the main dividing range from southern Queensland to eastern South Australia, also from islands in Bass Strait, and from Tasmania. It appears to be uncommon north of about the Hawkesbury River in New South Wales. Landlocked populations are known from New South Wales (L. Windimere), Victoria (many lakes) and South Australia (few). Populations that are probably freshwater-limited (they most closely resemble Victorian landlocked populations) occur in rivers draining to the south coast of Western Australia from the Goodja River eastwards to about Esperance.

Localities from which *G. maculatus* is known in Australia are indicated in Fig. 27, 28.

### **Galaxias occidentalis** Ogilby

Fig. 29

*Galaxias occidentalis* Ogilby, 1900: 157 (holotype: QM I.779, seen; paratypes: (2) AMS I.4175-6, I.4175 missing, other, seen; (1) BMNH 1905.7.29:10, not seen; type locality: streams south of Perth, Western Australia); Regan, 1905: 376; McCulloch, 1929: 47; Whitley, 1944: 265; 1947: 53; 1948: 11; Serventy, 1950: 165; Whitley, 1956a: 34; 1956b: 39: 1957a: 7; Munro 1957b: 15; Mees, 1961: 38; Gentilli, 1961: 488; Whitley, 1964: 35; Stokell, 1964: 46; Pollard, 1971b: 126; Lake, 1971: 20; 1978: 21.

TAXONOMY: There are no taxonomic problems associated with the identity and nomenclature of *G. occidentalis;* it is a valid species without any indication of more than one taxon being present. Although the species is widespread from north of Perth, south and east to the vicinity of Albany on the southern coast, there is little evidence of much regional variation (Tables 14, 15). The population from the Blackwood River has a somewhat higher vertebral count than that represented by samples from the vicinity of the Shannon River, but differences are in general small and difficult to interpret without much more extensive data and better understanding of the natural history of the species.

DIAGNOSIS: Characterised by elongate slender form, small, membranous fins, large mouth and distinctive broad dark vertical bars along sides. It differs from *G. maculatus* in characters listed in the diagnosis of that species (p.534). Differs from *G. rostratus* in having distinct lateral canine teeth in the jaws and a pair of fangs at the mandibular symphysis, a larger mouth and fewer anal fin rays.

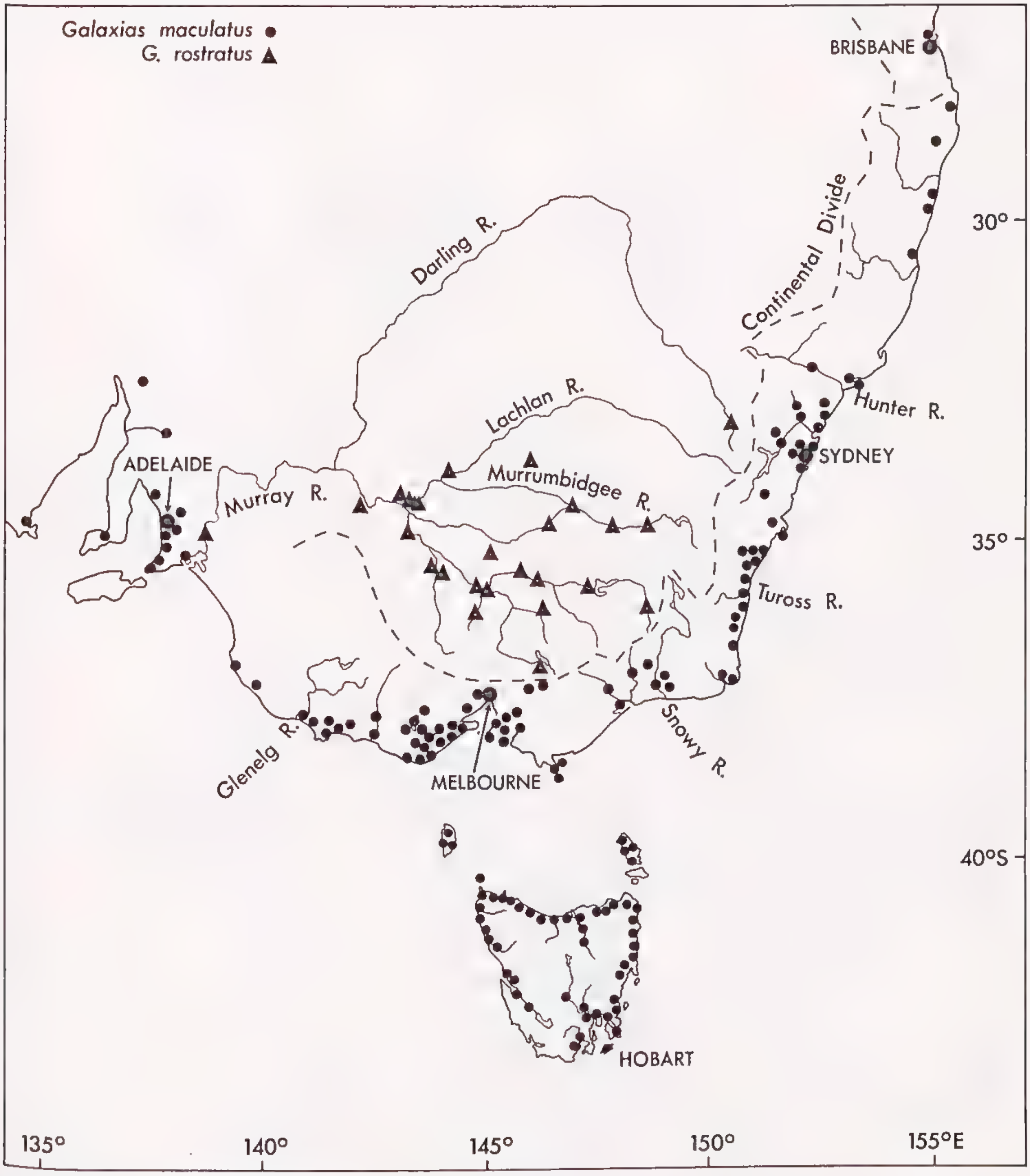

Fig. 27. Distribution of *Galaxias maculatus* (Eastern Australia) and *G. rostratus*. One symbol may represent more than one locality.

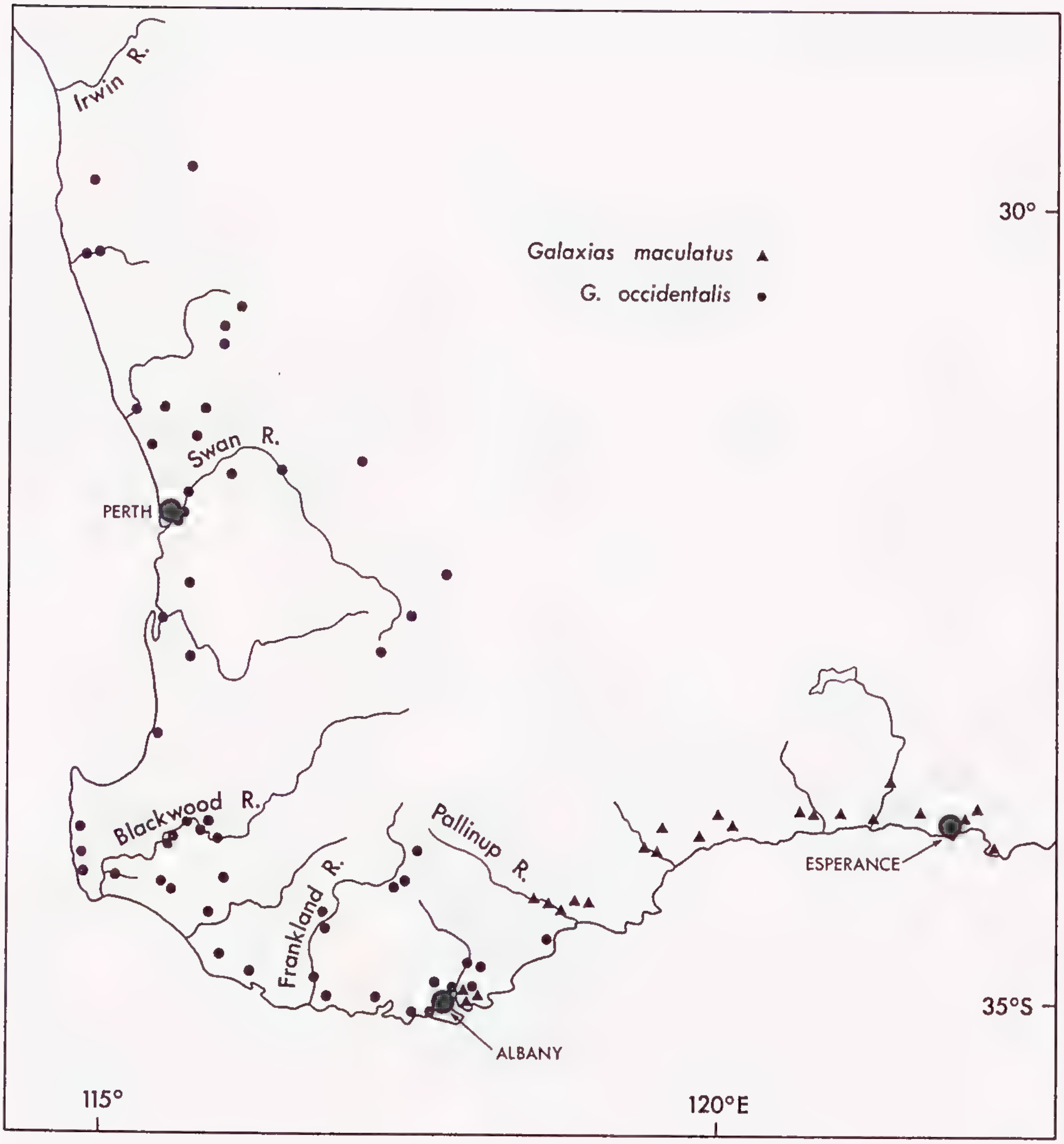

Fig. 28. Distribution of *Galaxias maculatus* (Western Australia) and *G. occidentalis*.

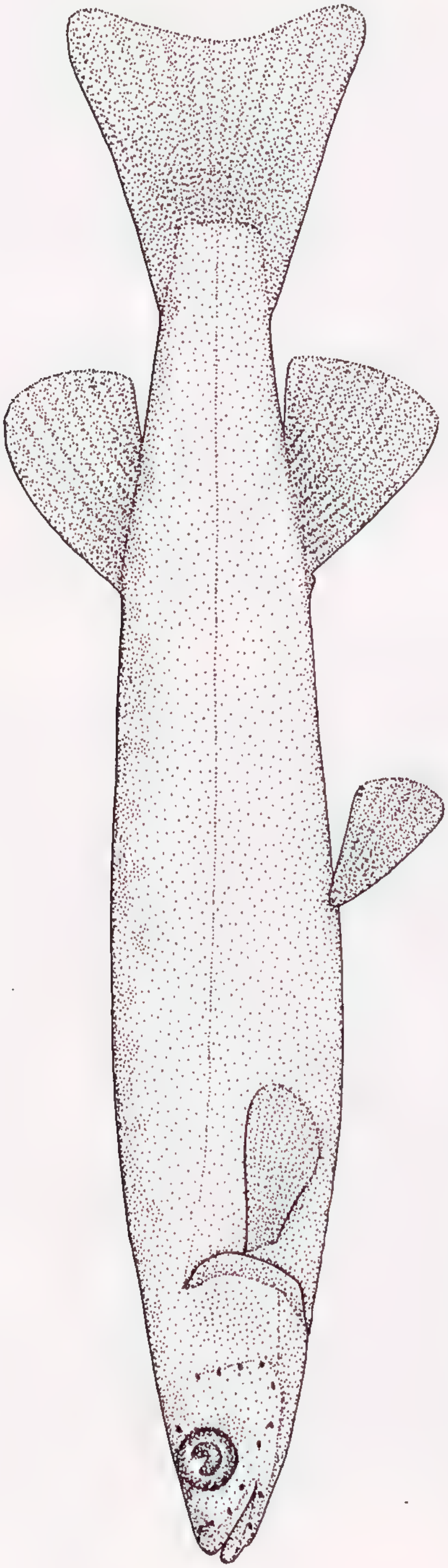

Fig. 29. *Galaxias occidentalis* Ogilby; Swan River, W.A., 73 mm L.C.F.

DESCRIPTION: A moderate-sized, elongate and slender-bodied species, somewhat compressed, with the dorsal and ventral trunk profiles slightly and evenly arched. Caudal peduncle of moderate length and very slender, depth much less than length. Head small, about as deep as broad, distinctly flattened dorsally. Snout long and tapering to slender, rounded point. Mouth moderate, oblique, large, reaching back to beyond front of eye, sometimes as far as middle of eye, lower jaw protruding slightly to distinctly. Eyes of moderate size, upper margins at about upper head profile, interorbital flat. Jaws with moderate to strong canines laterally, lower jaw with a pair of enlarged fangs at mandibular symphysis. Mesopterygoidal and lingual teeth very strong. Gill rakers long and relatively slender (Fig. 43); two short, round pyloric caeca (Fig. 45). Laterosensory pores on head as in Fig. 47; post-orbital pore has migrated antero-medially to lie in the interorbital.

Fins small and membranous. Dorsal and anal fins short-based, angular, maximum length of dorsal fin much greater than basal length but maximum length of anal little more than basal length; dorsal and anal origins about opposite or anal origin a little in front of dorsal. Pectoral fins very small, angular, with upper rays much the longest, fin tips rather pointed, insertion distinctly lateral, fin lamina vertical. Pelvic-anal interval long; pelvic fins very small, inserted at about mid-point of standard length. Caudal fin forked, fin tips only slightly rounded, fin depth rather less than body depth. Caudal peduncle flanges weakly developed.

Variation: meristic: see Table 14.
morphometric: see Table 15.

COLOUR: The back is greenish-olive, the sides similar with dark grey-black vertical bars, disposed in pairs, with the area between each of a pair somewhat paler than the area between pairs; the belly is silvery-white, the fins transluscent amber and the eye golden.

In preservative, greyish-white to brown, the back darker, the sides with very distinctive vertical markings which comprise narrow, unpigmented vertical bands bordered by dark bands, the broad area between the dark margins being somewhat paler. Thus there is a pigmentation sequence along the trunk of narrow, unpigmented band, dark margin, fading to grey, intensifying again to a dark margin followed by a further narrow, unpigmented band. Towards the tail these markings become less regular. The fins are largely unpigmented although the dorsal fin may be dusky at the base. The top of the head is darker, the belly unpigmented.

SIZE: *G. occidentalis* may reach a length of 166 mm L.C.F.; from material studied it evidently commonly reaches 80-100 mm.

HABITAT: Little has been reported on the habitat of *G. occidentalis.* In the Canning River, near Perth, it occurs "around submerged vegetation along the edges of pools or slow moving water, and also in rocky pools below small rapids in the faster flowing parts of the stream" (G. R. Allen, pers. comm.).

LIFE HISTORY: Nothing has been published, although it apparently spawns on vegetation in the headwaters of streams (A. R. Main, pers. comm.). There is nothing to indicate a marine stage in the life history of this species.

DISTRIBUTION: *G. occidentalis* occurs only in Western Australia, where it is widespread from about Winchester (250 km north of Perth) south and east to Waychinnicup Creek, 80 km north-east of Albany on the south coast (Fig. 28).

Table 14. Meristic variation in *Galaxias rostratus* and *G. occidentalis.*

| | | *G. rostratus* | | | | *G. occidentalis* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Colbinabbin, Vic | L. Wandella, Vic. | Rankins Lagoon, N.S.W. | Third Reedy Lake, Vic. | Twin Swamps, W.A. | Swan R., W.A. | Blackwood R., W.A. | Northcliffe R., W.A. | Shannon R., W.A. |
| Dorsal rays — segmented | 7 | | | | | | 1 | | | |
| | 8 | 1 | 1 | 1 | | | 3 | 5 | 5 | |
| | 9 | 7 | 7 | 3 | | | 4 | 5 | 5 | |
| | 10 | 6 | 8 | 1 | | | 2 | | | |
| total | 10 | | | 1 | | 2 | 1 | 3 | 5 | 1 |
| | 11 | 5 | 1 | 3 | 2 | 4 | 6 | 6 | 5 | 13 |
| | 12 | 9 | 12 | 0 | 5 | 1 | 3 | 1 | | |
| | 13 | 6 | 12 | 1 | | | | | | |
| Anal rays — segmented | 11 | 4 | 3 | 4 | | | 3 | 2 | | |
| | 12 | 9 | 8 | 1 | | | 3 | 5 | 5 | |
| | 13 | 2 | 3 | | | | 4 | 3 | 4 | |
| | 14 | | 0 | | | | | | 1 | |
| | 15 | | 1 | | | | | | | |
| total | 13 | | | | 1 | | | 1 | | |
| | 14 | 1 | 4 | 4 | 3 | | 4 | 1 | 2 | |
| | 15 | 8 | 7 | 1 | 1 | 4 | 1 | 4 | 4 | |
| | 16 | 9 | 11 | | 2 | 2 | 4 | 4 | 3 | 9 |
| | 17 | 2 | 2 | | | 1 | 1 | | 1 | 4 |
| | 18 | | 1 | | | | | | | 1 |
| Pectoral rays | 11 | 5 | 1 | 1 | 2 | | | | | |
| | 12 | 9 | 12 | 3 | 5 | 1 | 3 | 4 | 1 | |
| | 13 | 6 | 12 | 1 | | 6 | 6 | 3 | 5 | 2 |
| | 14 | | | | | | 1 | 2 | 3 | 10 |
| | 15 | | | | | | | 1 | 1 | 2 |
| Vertebrae | 50 | | | | | | | | | 1 |
| | 51 | | | | | | | | | 1 |
| | 52 | | | | | 2 | | | | 5 |
| | 53 | | 3 | | 1 | 4 | | 4 | | 5 |
| | 54 | 10 | 7 | | 5 | 1 | | 10 | | 2 |
| | 55 | 8 | 12 | | 1 | | | 7 | | |
| | 56 | 2 | 3 | | | | | 3 | | |
| | 57 | | | | | | | 1 | | |
| Gill rakers | 14 | 1 | | | | | | | | |
| | 15 | | | 1 | | | | | | |
| | 16 | 8 | 3 | 1 | | | 2 | | | |
| | 17 | 5 | 9 | 2 | | | 2 | 2 | 2 | |
| | 18 | 1 | 3 | 1 | | | 5 | 5 | 1 | |
| | 19 | | 1 | | | | 1 | 1 | 3 | |
| | 20 | | | | | | | 1 | 3 | |
| | 21 | | | | | | | 1 | 1 | |

Table 15. Morphometric variation in *Galaxias rostratus* and *G. occidentalis*. Figures are given as percentages of denominators in ratios.

| | *G. rostratus* — all data | | | | *G. occidentalis* | | | | | | Combined data | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Swan R., W.A. | | Northcliffe, W.A. | | Blackwood R., W.A. | | | | |
| | Min. | Mean | Max. | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Min. | Mean | Max. |
| S.L./T.L. | 87.6 | 89.14 | 91.4 | 0.84 | 89.99 | 0.63 | 89.65 | 1.03 | 88.84 | 0.85 | 87.8 | 89.46 | 91.0 |
| B.D.V./S.L. | 10.1 | 11.85 | 14.2 | 0.91 | 11.90 | 0.38 | 11.70 | 0.62 | 12.30 | 0.68 | 10.7 | 12.02 | 13.3 |
| L.C.P./S.L. | 10.6 | 12.86 | 14.6 | 0.96 | 14.11 | 0.70 | 13.22 | 0.69 | 13.96 | 0.45 | 11.6 | 13.76 | 15.4 |
| D.C.P./L.C.P. | 40.0 | 55.61 | 68.8 | 6.27 | 51.43 | 2.95 | 58.37 | 4.71 | 54.96 | 1.98 | 47.1 | 54.92 | 68.0 |
| Pre. D./S.L. | 71.6 | 73.86 | 77.3 | 1.33 | 73.47 | 1.42 | 74.35 | 1.19 | 75.33 | 0.93 | 71.3 | 74.38 | 76.9 |
| Pre. D./Pre A. | 92.7 | 96.14 | 99.3 | 1.65 | 99.90 | 1.95 | 100.60 | 1.67 | 101.15 | 1.51 | 96.3 | 100.55 | 103.6 |
| L.D.B./S.L. | 7.6 | 9.06 | 11.0 | 0.81 | 8.42 | 0.96 | 8.31 | 0.74 | 7.85 | 0.62 | 6.9 | 8.19 | 10.2 |
| M.L.D./L.D.B. | 128.9 | 157.77 | 200.0 | 14.03 | 177.81 | 18.55 | 172.44 | 11.99 | 177.90 | 13.32 | 150.0 | 176.05 | 211.1 |
| L.A.B./S.L. | 9.7 | 11.56 | 15.7 | 1.08 | 12.92 | 0.83 | 13.94 | 1.02 | 12.41 | 0.82 | 11.0 | 13.09 | 15.5 |
| M.L.A./L.A.B. | 112.8 | 130.23 | 164.3 | 12.05 | 128.30 | 6.09 | 124.47 | 6.80 | 132.06 | 6.18 | 111.9 | 128.28 | 146.7 |
| Pec./Pec.Pel. | 34.0 | 41.29 | 50.0 | 4.84 | 46.28 | 2.84 | 42.30 | 2.51 | 41.72 | 3.47 | 35.7 | 43.43 | 50.8 |
| Pel./Pel.An. | 31.7 | 40.33 | 47.1 | 3.11 | 49.17 | 2.63 | 44.14 | 4.05 | 43.83 | 3.24 | 36.5 | 45.71 | 51.9 |
| Pre.Pel/S.L. | 45.2 | 50.71 | 53.2 | 1.72 | 50.25 | 1.10 | 50.30 | 1.23 | 50.12 | 1.35 | 47.7 | 50.22 | 52.6 |
| Pec. Pel./S.L. | 24.6 | 28.23 | 31.2 | 1.34 | 27.63 | 0.94 | 29.14 | 1.25 | 29.19 | 1.50 | 26.3 | 28.65 | 31.5 |
| Pel.An./S.L. | 23.6 | 26.75 | 28.9 | 1.26 | 23.39 | 0.68 | 24.45 | 0.82 | 25.20 | 1.25 | 22.4 | 24.35 | 26.8 |
| H.L./S.L. | 21.8 | 23.06 | 24.4 | 0.69 | 22.89 | 0.92 | 21.28 | 0.56 | 22.22 | 0.46 | 20.1 | 22.13 | 24.4 |
| H.W./H.L. | 45.3 | 47.71 | 52.3 | 2.02 | 47.89 | 1.84 | 55.07 | 3.25 | 52.37 | 1.26 | 45.5 | 51.78 | 59.5 |
| H.D./H.L. | 44.6 | 49.86 | 54.5 | 2.41 | 50.40 | 1.80 | 54.53 | 2.45 | 52.69 | 2.28 | 48.3 | 52.54 | 58.3 |
| Sn.L./H.L. | 25.8 | 29.04 | 32.6 | 1.66 | 32.99 | 2.46 | 31.50 | 1.97 | 31.19 | 2.11 | 27.4 | 31.89 | 38.0 |
| P.O.H.L./H.L. | 50.0 | 53.76 | 58.1 | 1.85 | 51.75 | 1.85 | 51.94 | 2.04 | 52.59 | 2.98 | 48.7 | 52.09 | 57.1 |
| I.O.W./H.L. | 32.5 | 34.63 | 36.4 | 1.23 | 35.49 | 2.34 | 35.13 | 2.25 | 36.05 | 2.16 | 31.3 | 35.56 | 40.0 |
| D.E./H.L. | 18.8 | 20.82 | 25.0 | 1.38 | 25.48 | 2.00 | 22.77 | 2.88 | 22.93 | 1.86 | 18.6 | 23.73 | 30.0 |
| L.U.J./H.L. | 32.3 | 35.71 | 40.9 | 1.99 | 44.33 | 2.90 | 43.89 | 3.91 | 42.00 | 1.86 | 38.2 | 43.41 | 51.7 |
| L.M./H.L. | 31.0 | 34.48 | 39.7 | 2.12 | 45.05 | 3.83 | 45.29 | 3.02 | 43.83 | 2.11 | 37.9 | 44.72 | 50.0 |
| W.G./H.L. | 25.0 | 27.89 | 33.3 | 1.90 | 29.42 | 1.58 | 35.68 | 2.20 | 30.96 | 2.31 | 27.3 | 32.02 | 40.5 |
| N | | 35 | | | 10 | | 10 | | 10 | | | 30 | |

### **Galaxias rostratus** Klunzinger, 1872
Fig. 30

*Galaxias rostratus* Klunzinger, 1872: 41 (lectotype: AMS I.19743-001, formerly SMNS 1597, seen; paralectotypes: (2) SMNS 1597, seen, (1) AMS I.19743-002, formerly SMNS 1597, seen; type locality: Murray River); 1880: 412; Macleay, 1881: 47; 1886: 55; Ogilby, 1896: 69; Lucas, 1890: 46; Regan, 1905: 378; McCulloch, 1929: 48; Whitley, 1944: 264; Stokell, 1947: 67; Whitley, 1956a: 34; 1956b: 39; 1957a: 7; Munro, 1957b: 16; Lake, 1978: 24; Backhouse and Vanner, 1978: 128:

*Galaxias planiceps* Macleay, 1881: 233 (syntypes: formerly (9) MMS F.85, now (6) AMS I.16261-001, seen; type locality: Rankins Lagoon, near Bathurst, New South Wales); Tenison-Woods, 1883: 22; Ogilby, 1886: 54; 1896: 69; Waite, 1904: 17; McCulloch, 1921: 28; 1922: 18; 1927: 18; 1929: 49; Mack, 1936: 100; Whitley, 1956a: 34; 1956b: 39; 1957a: 7; Munro, 1957b: 15; Gentilli, 1961: 488; Whitley, 1964: 35; Lake, 1967: 14; Stanbury, 1969: 205; Llewellyn, 1969: 16; Lake, 1971: 20; Frankenberg, 1971: 95; Pollard, 1971b: 126; Llewellyn, 1971: 10; 1973: 91; 1974: 147; Chessman and Williams, 1974: 170.

*Galaxias waitii* Regan, 1905; 376 (syntypes: (4) BMNH 1905.7.29: 2-5, seen; there are also 12 specimens AMS I.7411-14, labelled as syntypes, which were sent to the Australian Museum by Regan, in 1905. They are from the type locality but Regan explicitly stated that he based his description on four specimens which are therefore the only syntypes; type locality; Gulpa Creek, New South Wales); Whitley, 1956a: 34.

*Galaxias (Galaxias) rostratus* — Scott, 1936: 90.

*Galaxias planiceps waitii* — Whitley, 1964: 35.

TAXONOMY: The syntypes of *G. rostratus* were re-located at the Staatl Museum für Naturkunde by Dr J. R. Paxton, in 1976. Hitherto they were unknown to ichthyologists interested in galaxiid fishes, and placement of the species in synonymies had been uncertain. Most authors ignored the species but Munro (1957b) regarded it as "Possibly the same as" *G. planiceps*, and Lake (1971) listed both *G. rostratus* and *G. planiceps*. The specimens were taken to Sydney by Dr D. F. Hoese and some of them re-deposited in the Australian Museum.

Examination of the syntypes of *G. rostratus* has shown that Munro's (1957b) opinion was correct. They have large mouths reaching well below the eye, slightly to distinctly protruding lower jaws, long snouts, distinctly flattened heads and low vertebral counts (53 vertebrae — 2 fish, 55 — 2 fish), this combination of characters agreeing with the syntypes of *G. planiceps* and with the species hitherto known by that name in Australia. One of the syntypes (113.5 mm S.L.) has been chosen as lectotype and re-deposited in the collection of the Australian Museum, with the approval of the Director of the Staatl Museum für Naturkunde.

Samples of *G. rostratus* are relatively few and mostly old. Examination of existing material from the Murray-Darling system, including that described by Regan (1905) as *G. waitii*, does not indicate the presence of more than one species. The *G. waitii* of Regan are indistinguishable from *G. rostratus;* Regan (1905) made no reference to *G. rostratus*, or, for that matter, to *G. planiceps*, in his revision of the family and was apparently unaware of their descriptions.

DIAGNOSIS: *G. rostratus* is characterised by the combination of flat head, large mouth reaching below eyes, very small pectoral and pelvic fins, forked caudal fin, the absence of pyloric caeca and lack of lateral canine teeth in the jaws. It most closely

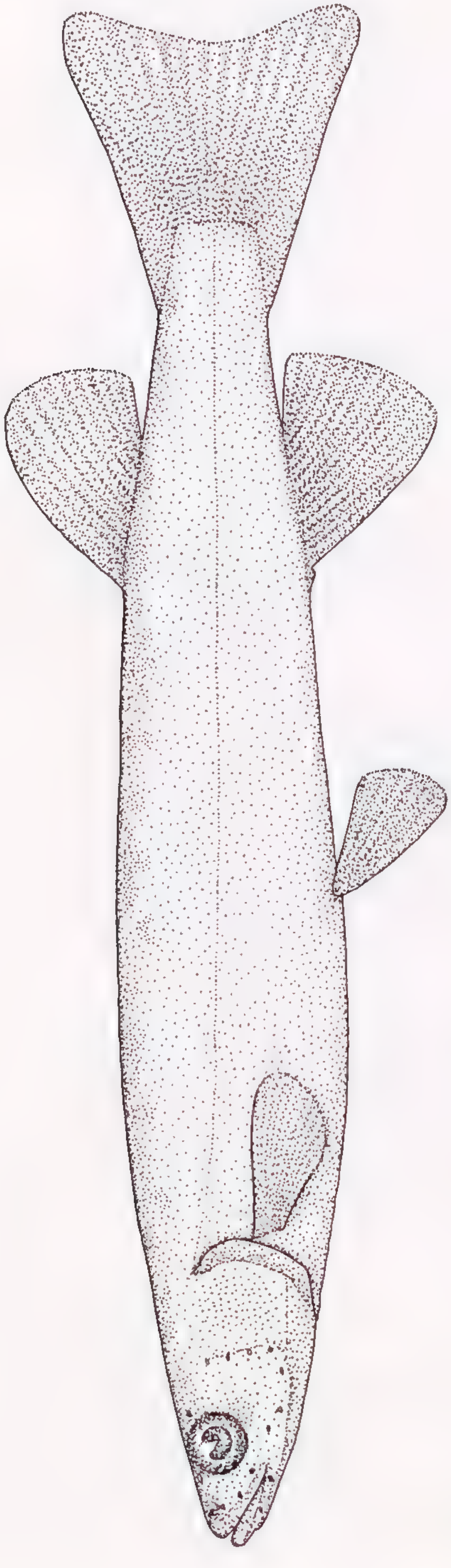

Fig. 30. *Galaxias rostratus* Klunzinger; Wandella Lake, Vic., 79 mm L.C.F.

resembles *G. maculatus* and *G. occidentalis* and differs from these species in characters listed in their diagnoses (pp.534 and 542 respectively.

DESCRIPTION: A moderate-sized elongate and slender-bodied species somewhat compressed along whole trunk, belly little deepened, trunk profiles about parallel in front of dorsal fin but tapering to a slender caudal peduncle which is longer than deep. Head of moderate length, flattened dorsally but about as deep as broad, cheeks not broadening below eyes. Snout flattened and slender, moderately pointed. Mouth slightly oblique, large, extending to below about middle of eyes, lower jaw variable in length, equal to upper or slightly to distinctly protruding. Eyes of moderate size, towards upper head profile, inter-orbital flat. Jaws without lateral canines; mesopterygoidal teeth well developed; gill rakers of moderate length and quite stout (Fig. 43); no pyloric caeca (Fig. 45). Laterosensory pores on head as in Fig. 47.

Fins small, not fleshy at bases. Dorsal fin short-based, rather angular, fin extending well back from base; anal fin origin below or a little behind dorsal origin, longer-based and lower than dorsal, hindmost rays much shorter than anterior ones, fin extending back little beyond base. Pectoral fins small and paddle-shaped, insertion distinctly lateral; pelvic-anal interval long, pelvic fins very short, inserted at about mid-point of standard length. Caudal fin with a distinct but shallow fork, fin tips rounded, fin depth about equal to body depth, peduncle flanges well developed.

Variation: meristic: see Table 14.
morphometric: see Table 15.

COLOUR: When alive greenish-olive on the back and sides, with irregular darker grey-green blotches, the sides below the lateral line bright silvery; the fins are colourless and the eyes silver.

In preservative the fish are dull cream to brown with irregular and rather indistinct blotching on the back and sometimes a strong dark line along the lateral line.

SIZE: *G. rostratus* grows to about 130 mm L.C.F. (Llewellyn, 1971) and not uncommonly exceeds 100 mm.

HABITAT: Little has been recorded, but *G. rostratus* seems to be taken mostly in still and gently flowing waters — lakes, lagoons, billabongs and backwaters, where it occurs in shoals, in midwater.

LIFE HISTORY: Llewellyn (1971) reported on the spawning of *G. rostratus* in ponds. He found that spawning occurs at relatively cool temperatures (9-14°C). The eggs are small (1.3-1.6 mm in diameter) and fecundity is several thousand eggs per female. The eggs are spawned randomly in midwater and settle to the bottom; development takes about 9 days and the larvae are 6-7 mm long at hatching. Llewellyn (p. 11) found that breeding "appears to continue for up to a month suggesting that only small numbers of eggs are shed by any one fish at a time". If true, this is different from what little is known of other galaxiids; however, Llewellyn did not document his findings.

DISTRIBUTION: *G. rostratus* is known only from the Murray-Darling River system, where it is widespread, although of intermittent occurrence (Fig. 27).

### **Galaxias scottii** Krefft *Nomen nudum*

*Galaxias scottii* Krefft, 1871: 84 (types and type locality not indicated, no description given); Ogilby, 1886: 55; McCulloch, 1929: 55.

## Genus **Galaxiella** McDowall

TYPE SPECIES: *Galaxias pusillus* Mack, 1936: 101, by original designation.

DIAGNOSIS: Small, stocky galaxiid fishes with dorsal fin origin posterior, behind vent and anal fin origin. Pelvic fins present, usually 4-6 rays (range 4-7); pectoral fins inserted high laterally. Caudal fin rounded, usually with 13-14 principal rays (range 12-15); caudal peduncle flanges very strongly developed but with very few procurrent rays. No submandibular laterosensory pores. No median ethmoid ossification. Postcleithrum present. Epipleural and epineural ribs present; no ossified interneurals. Caudal neural and haemal spines slender spikes, not laterally flattened. Vertebrae few, 38-43; branchiostegals few, 3-4.

### KEY TO SPECIES OF GALAXIELLA

1. Usually 6 pelvic fin rays (range 5-7); usually 10-11 pectoral fin rays (range 9-12); gill rakers long and slender, 16-20; body depth at vent/standard length ratio 10.5-14.3%. (Western Australia from Albany to north of (Perth). ........................................................................... *G. munda* p.565.

   Usually 5 pelvic fin rays (range 4-6); usually 12-13 pectoral fin rays (range 10-14; gill rakers of moderate length, 14-17; body depth at vent/standard length ratio 13.5-18.6%

2. Usually 9-10 segmented anal fin rays (range 8-11); usually 13 caudal fin rays (range 12-14); 8 pores in preopercular-suborbital-supramaxillary series; 3 distinct lateral longitudinal stripes. (Bass Strait coasts of South Australia, Victoria and Tasmania.) ........................................................ *G. pusilla* p.552.

   Usually 11-13 segmented anal rays (range 10-15); usually 14 caudal fin rays (range 12-15); 9 pores in pre-opercular-suborbital-supramaxillary series; 2 distinct lateral longitudinal dark stripes. (Western Australia along the south coast.) ............................................................... *G. nigrostriata* p.562.

### **Galaxiella pusilla** (Mack)

Fig. 31, 32.

*Galaxias pusillus* Mack, 1936: 101 (holotype: NMVM A.97 seen; paratypes: (4) NMVM A. 98 and A.388-90, seen; type locality: Cardinia Creek, Victoria); Stokell, 1945: 126; McDowall, 1971: 37; 1973c: 193; Andrews, 1976: 324.

*Brachygalaxias pusillus* — Massola, 1938: 129; Scott, 1942: 55; Stokell, 1954: 412; Whitley, 1956a: 34; 1956b: 39; 1957a: 6; 1960: 29; 1964: 34; Scott, 1966: 246; Frankenberg, 1966a: 162; 1966b: 32; 1968: 162; Lake, 1971: 20; Dixon, 1972: 121; Chessman and Williams, 1974: 270.

*Brachygalaxias pusillus pusillus* — Shipway, 1953: 175; Munro, 1957a: 18; Frankenberg, 1971: 94; Scott, 1971a: 4.

*Brachygalaxias pusillus tasmaniensis* Scott, 1971a: 3 (holotype: QVML 1971.5.48a, seen; paratypes: (11) QVML 1971.5.48b, seen; BMNH 1972.1.27: 2, not seen; (1) AMS I.16159-001, seen; type locality: soak from dam flowing towards the coast (northward) on Marengo, Waterhouse Estate, Dorset, Tasmania); Green, 1974: 3; Frankenberg, 1974: 119.

*Brachygalaxias pusillus flindersiensis* Scott, 1971a: 6 (holotype: QVML 1969.5.25a, seen; paratypes: (14) QVML 1969.5.25b, seen; (1) BMNH 1972.1.27: 1, not seen; (1) AMS I.16158-001, seen; type locality: Lackrana, Flinders Island, Bass Strait); Frankenberg, 1974: 119.

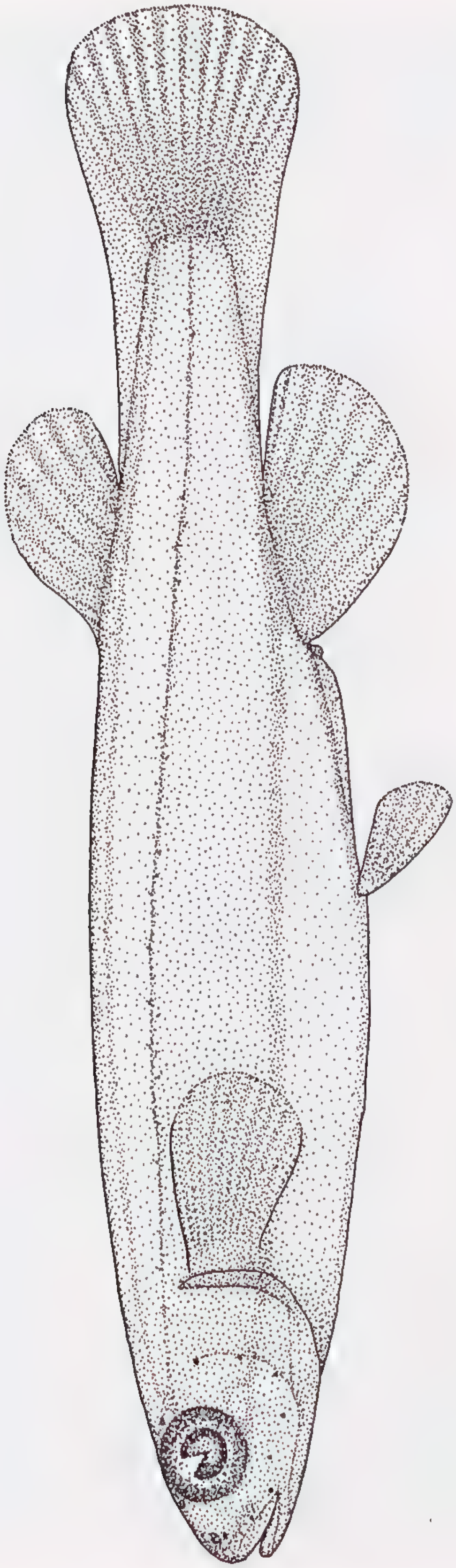

Fig. 31. *Galaxiella pusilla* (Mack), Narracan Creek, Vic., 28.5 mm T.L.

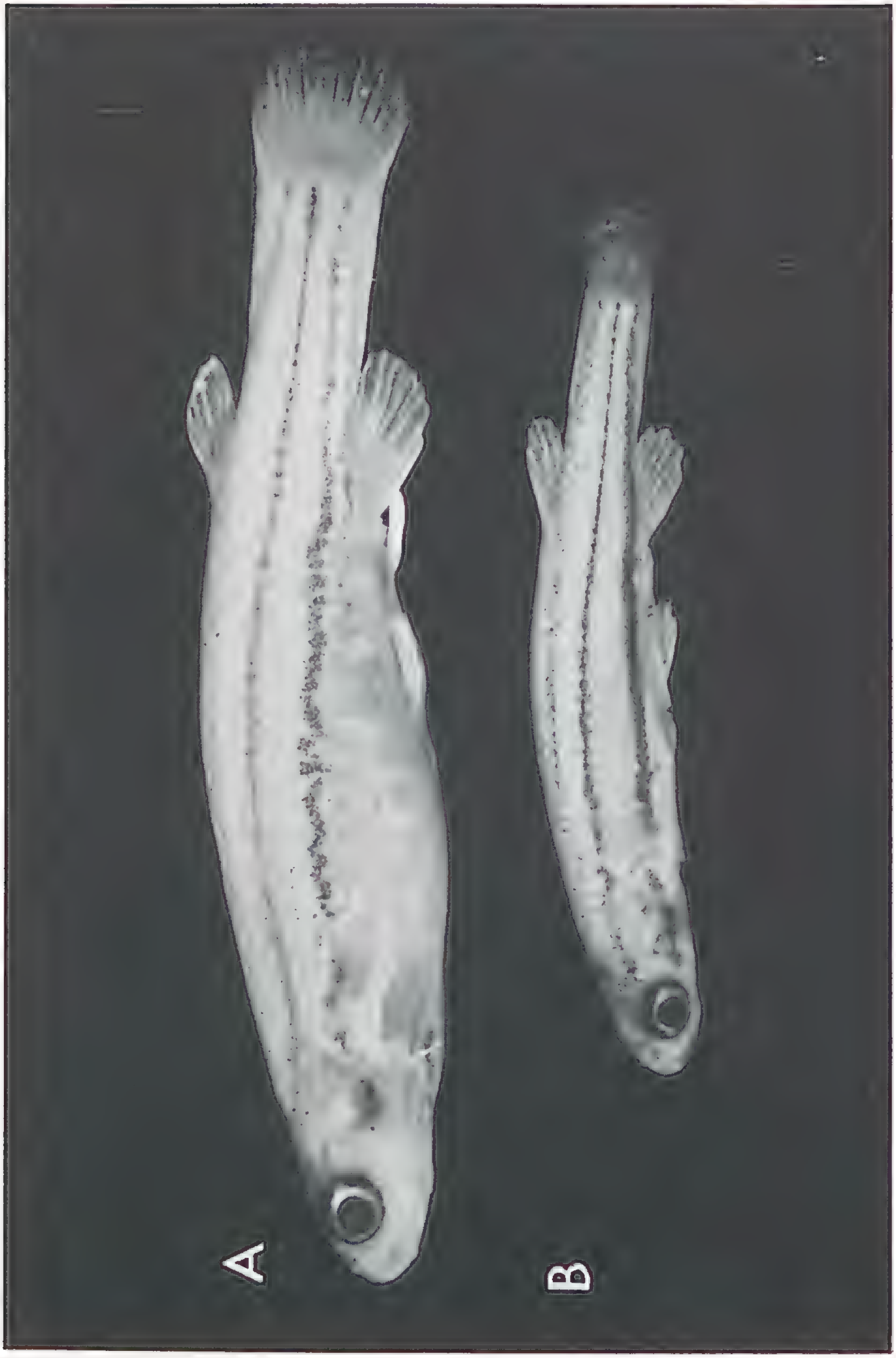

Fig. 32. *Galaxiella pusilla* (Mack), Narracan Creek, Vic., **a.** female — 36 mm T.L.; **b.** male — 25 mm T.L.

*Galaxias nigrostriatus* — McDowall, 1973: 197 (non *G. nigrostriatus* Shipway, 1953: 175 ??).

*Galaxiella pusilla* — McDowall, 1978a: 119; 1978b: 308; Lake, 1978: 26; Backhouse and Vanner, 1978: 128.

TAXONOMY: Inclusion of this and the subsequent two species in *Galaxiella* rather than *Galaxias* Cuvier or *Brachygalaxias* Eigenmann is discussed in the generic section on p.454.

Scott (1971a) described two new sub-species of *G. pusilla* as *Brachygalaxias pusillus tasmaniensis* and *B. pusillus flindersiensis* from Tasmania and Flinders Island respectively. Although Scott did not describe the nominate sub-species *B. pusillus pusillus* from Victoria, he did indicate the differences between it and the new sub-species. He reported differences in such characters as head length, snout length, eye diameter, vertebral count, etc., and showed that there are statistically significant differences between the populations he examined. That these differences have little taxonomic significance was shown by Andrews (1976). He examined more material from a greater range of geographical localities and found that rather than there being differences between sets of populations from the three geographical areas nominated by Scott (1971a) there are similar differences between populations within each of these geographical areas. When the more extensive range of material examined by Andrews is combined for each of Victoria, Flinders Island and Tasmania, the supposed differences between the sub-species from each of these areas largely disappear. Andrews treated all three sub-species as synonyms, and his arrangement is adopted here.

As an example of the sorts of differences used by Scott (1971a) we cite the following: Scott (1971a: 7) stated "Perhaps the nearest approach to a definitive criterion for the separation of individuals of, on the one hand, the Victorian forms, on the other hand the Tasmanian and Flinders Island forms, is that of number of ventral fin rays. This is specified in the description of *B. p. pusillus* as 5, and appears seldom to depart from that number whereas a count of 4 was obtained in 13 of the 14 Tasmanian fish and in all of the Flinders Island examples examined". However, we have found 5 rays to predominate in a sample of *G. pusilla* from Tasmania and 4 rays to predominate in some Victorian populations. Further, the population at Eumaralla, Victoria, has 36-38 vertebrae, that nearby at Tyabb 37-40, a population at Narracan Creek, Victoria 38-40, while that at Blackmans Lagoon, Tasmania has 37-40. Variation of this type, as discussed by Andrews (1976), appears to have no logical basis, and understanding of the reasons for it must await collection of more adequate and widely representative material. Recognition of sub-species on the basis of such variation would seem to have little meaning.

Reasons for the exclusion from *G. pusilla* of Western Australian populations of *Galaxiella* that are sometimes described as a sub-species of *G. pusilla* (see Shipway, 1953; Munro, 1957a) are given in the taxonomic discussion of *G. nigrostriata*.

DIAGNOSIS: Characterised by the dorsal origin behind the anal origin, small size, absence of laterosensory pores beneath the lower jaw, and presence of three longitudinal dark stripes along the sides, the lower two separated (in life) by a bright orange stripe in males. In the small size and lack of pores beneath the lower jaw it resembles species of *Paragalaxias*, but differs from them in having the dorsal fin above the anal (above the pelvics in *Paragalaxias*). *G. pusilla* closely resembles other species of *Galaxiella;* it differs from *G. nigrostriata* in having fewer caudal and pelvic fin rays (Table 16), and in having three rather than two longitudinal dark stripes. It has fewer laterosensory pores in the preopercular-supramaxillary series (Fig. 47). It differs from *G. munda* in being stouter, having a shorter based anal fin, fewer anal, caudal and pelvic fin rays, fewer gill rakers and vertebrae, and more pectoral fin rays (see Table 16). There are no really distinct lateral dark stripes in *G. munda* although there is a broader dusky band split by a narrow, pale (in preserved specimens), crenulate stripe along the lower sides.

DESCRIPTION: A tiny, fusiform species, compressed behind the vent, the dorsal and ventral body profiles moderately and evenly arched, body depth greatest at about mid-abdomen. Caudal peduncle long and deep, much longer than deep. Head short, broad and deep, about as broad as deep. Snout short and bluntly rounded. Mouth small, oblique, reaching back almost to front of eyes; jaws about equal. Eyes large, upper margin at about head profile; interorbital broad and flat. Jaws without enlarged lateral canines; mesopterygoidal teeth few but strong; lingual teeth well developed. Gill rakers long and slender (Fig. 44); pyloric caeca lacking (Fig. 46). Laterosensory pores on head as in Fig. 47. No submandibular pores; eight pores in preopercular-supramaxillary series with a distinct "dog-leg" in row beneath eye (fourth to seventh pores); pores in anterior nasal depression distinctly posterior to nostril.

Fins all small and membranous, dorsal and anal fins short-based, rounded, posterior rays extending back moderately behind fin bases; anal fin origin distinctly in front of dorsal origin. Pectoral fins broad-based, small and rounded, insertion high laterally, fin lamina distinctly lateral. Pelvic-anal interval very short; pelvic fins very small, inserted at about mid-point of standard length. Caudal fin long and rounded, depth about equal to length, somewhat less than body depth. Caudal peduncle flanges strongly developed and reaching forward to be more or less confluent with dorsal and anal fin bases; few procurrent caudal fin rays.

Variation: meristic: see Table 16.
morphometric: see Table 17.

SEXUAL DIMORPHISM: Sexual dimorphism has been described for *G. pusilla;* Massola (1938) pointed to differences in colouration between the sexes, but these differences were not mentioned by most subsequent workers (Scott, 1971; Andrews, 1976; McDowall, 1973c; 1978a — see however, Backhouse and Vanner, 1978), probably because of the meagre samples available. Observations of live material confirmed differences between the sexes in colour, and comparisons of measurements also indicated differences in size and in some body proportions (McDowall, 1978b) as follows: 1. Size: Males are smaller than females (Table 18, Fig. 32). 2. Body proportions: Ripe males are more slender-bodied than ripe females, this being primarily a reflection of the swollen abdomens of the ripe females, and this difference has little significance (Table 18). The pectoral-pelvic and pelvic-anal dimensions in males are less than in females (Table 18). Examination of plots of pectoral-pelvic length/standard length and pelvic-anal length/standard length suggested that there is allometric growth in this fish; the higher ratios in females are produced by allometry common to the two sexes, but which continues further in females than in males because the females grow to a greater size (Fig. 33). 3. Ventral keel and genital papilla: In both sexes there is a fleshy/horny keel along the ventral abdomen, beginning at about the pelvic fin bases, and extending back as far as the vent. The depth of the keel is slightly greater in males than in females, although the difference is slight. In the male, the vent is followed by a low fleshy genital papilla that projects slightly more than the vent; in the female the genital papilla is a distinct fleshy mound. 4. Colouration also varies between the sexes (see "Colour", below).

*G. pusilla* is the only species in the family Galaxiidae in which sexual dimorphism has been described, although it may occur in other *Galaxiella* species; existing material does not suffice to determine this.

Table 16. Meristic variation in *Galaxiella* species.

| | | *G. pusilla* | *G. nigrostriata* | *G. munda* |
|---|---|---|---|---|
| Dorsal fin rays — segmented | 5 | 1 | | |
| | 6 | 18 | 10 | 8 |
| | 7 | 24 | 10 | 24 |
| | 8 | 3 | | 5 |
| total | 6 | 1 | | |
| | 7 | 14 | 3 | 1 |
| | 8 | 23 | 11 | 18 |
| | 9 | 8 | 6 | 15 |
| | 10 | | | 3 |
| Anal rays — segmented | 7 | 13 | | |
| | 8 | 24 | 2 | |
| | 9 | 9 | 11 | 1 |
| | 10 | 1 | 3 | 12 |
| | 11 | | 3 | 19 |
| | 12 | | | 5 |
| total | 8 | 9 | | |
| | 9 | 22 | | |
| | 10 | 12 | 2 | |
| | 11 | 4 | 7 | 1 |
| | 12 | | 6 | 5 |
| | 13 | | 2 | 16 |
| | 14 | | 1 | 13 |
| | 15 | | 1 | 2 |
| Caudal rays | 12 | 8 | 1 | |
| | 13 | 39 | 4 | 1 |
| | 14 | 1 | 14 | 32 |
| | 15 | | 1 | 2 |
| Pectoral rays | 9 | | | 1 |
| | 10 | 3 | | 15 |
| | 11 | 8 | 3 | 9 |
| | 12 | 25 | 14 | 3 |
| | 13 | 9 | 4 | |
| | 14 | 2 | 1 | |
| Pelvic rays | 4 | 16 | | |
| | 5 | 27 | 19 | 2 |
| | 6 | 1 | | 33 |
| | 7 | | | 2 |
| Gill rakers | 12 | 3 | | |
| | 13 | 2 | | |
| | 14 | 8 | 1 | |
| | 15 | 5 | 4 | |
| | 16 | 8 | 9 | 5 |
| | 17 | 1 | 2 | 4 |
| | 18 | | 2 | 3 |
| | 19 | | | 3 |
| | 20 | | | 1 |
| Vertebrae | 36 | 2 | | |
| | 37 | 4 | | |
| | 38 | 6 | 2 | 3 |
| | 39 | 25 | 22 | 7 |
| | 40 | 9 | 14 | 15 |
| | 41 | | 8 | 18 |
| | 42 | | 3 | 19 |
| | 43 | | 2 | 4 |

Table 17. Morphometric variation in *Galaxiella* species.
Figures are given as percentages of denominators in ratios.

| | *G. pusilla* | | | | *G. nigrostriata* | | | | *G. munda* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Min. | Mean | Max. | S.D. | Min. | Mean | Max. | S.D. | Min. | Mean | Max. | S.D. |
| Standard length/total length | 83.1 | 86.59 | 89.2 | 1.52 | 83.7 | 85.88 | 90.3 | 1.75 | 82.2 | 84.91 | 87.7 | 1.29 |
| Body depth at vent/standard length | 13.8 | 15.51 | 18.6 | 1.35 | 13.5 | 16.48 | 18.5 | 1.21 | 10.5 | 12.83 | 14.3 | 1.12 |
| Length of caudal peduncle/standard length | 20.3 | 22.37 | 24.3 | 1.71 | 18.7 | 20.98 | 23.5 | 1.51 | 15.2 | 18.93 | 22.5 | 1.73 |
| Depth of caudal peduncle/length of peduncle | 41.7 | 49.19 | 55.5 | 4.98 | 46.4 | 55.78 | 61.9 | 4.31 | 40.7 | 47.30 | 54.5 | 4.69 |
| Predorsal length/standard length | 70.1 | 72.75 | 79.0 | 2.31 | 70.5 | 72.56 | 75.0 | 1.04 | 70.2 | 73.29 | 76.7 | 1.41 |
| Predorsal length/pre anal length | 101.5 | 107.06 | 112.1 | 2.81 | 104.7 | 107.82 | 112.5 | 1.98 | 105.0 | 108.30 | 111.9 | 1.87 |
| Length of dorsal fin base/standard length | 5.9 | 7.8 | 10.3 | 0.94 | 7.1 | 7.88 | 8.8 | 0.61 | 6.7 | 8.30 | 9.8 | 0.73 |
| Maximum length of dorsal fin/basal length | 155.6 | 184.62 | 200.0 | 14.85 | 155.6 | 175.32 | 188.2 | 10.33 | 150.0 | 174.47 | 200.0 | 13.91 |
| Length of anal fin base/standard length | 8.1 | 10.36 | 12.6 | 1.38 | 11.1 | 12.58 | 13.8 | 0.88 | 12.3 | 14.63 | 16.4 | 1.07 |
| Maximum length of anal fin/basal length | 133.2 | 155.49 | 190.0 | 16.36 | 128.6 | 144.09 | 166.7 | 10.40 | 125.0 | 137.17 | 154.5 | 7.84 |
| Pectoral fin length/pectoral-pelvic length | 42.9 | 51.75 | 61.5 | 6.42 | 41.2 | 47.84 | 51.6 | 3.06 | 39.1 | 45.17 | 52.9 | 3.58 |
| Pelvic fin length/pelvic-anal length | 42.9 | 51.87 | 68.8 | 7.11 | 50.0 | 60.38 | 68.8 | 5.03 | 50.0 | 60.34 | 70.0 | 5.66 |
| Prepelvic length/standard length | 45.5 | 49.93 | 53.7 | 2.23 | 46.1 | 50.63 | 52.8 | 1.64 | 40.5 | 49.12 | 52.6 | 3.04 |
| Pectoral-pelvic length/standard length | 23.7 | 29.61 | 34.8 | 3.31 | 27.4 | 29.51 | 31.8 | 1.19 | 23.2 | 29.41 | 33.3 | 2.38 |
| Pelvic-anal length/standard length | 16.2 | 19.54 | 22.2 | 1.52 | 15.0 | 16.55 | 17.9 | 0.90 | 15.5 | 17.60 | 19.7 | 1.08 |
| Head length/standard length | 21.4 | 22.73 | 24.7 | 0.83 | 20.9 | 22.38 | 23.9 | 0.82 | 17.4 | 19.90 | 22.8 | 1.16 |
| Head width/head length | 54.5 | 60.79 | 65.5 | 2.82 | 53.8 | 59.43 | 66.7 | 4.32 | 50.0 | 55.75 | 62.5 | 3.40 |
| Head depth/head length | 52.0 | 59.04 | 62.5 | 3.24 | 55.5 | 60.29 | 66.7 | 3.15 | 50.0 | 55.88 | 66.7 | 4.16 |
| Snout length/head length | 24.0 | 26.99 | 30.4 | 1.63 | 22.2 | 26.43 | 29.6 | 1.93 | 23.1 | 28.21 | 35.0 | 2.49 |
| Post-orbital head length/head length | 42.4 | 48.04 | 54.8 | 3.20 | 44.4 | 48.38 | 54.2 | 2.71 | 41.7 | 46.54 | 53.6 | 2.34 |
| Interorbital width/head length | 32.0 | 38.77 | 45.5 | 3.66 | 33.3 | 37.89 | 44.5 | 3.36 | 34.4 | 40.80 | 45.8 | 2.67 |
| Diameter of eye/head length | 25.8 | 29.49 | 34.8 | 2.66 | 25.0 | 28.26 | 30.8 | 1.57 | 26.5 | 30.40 | 35.0 | 2.41 |
| Length of upper jaw/head length | 24.0 | 28.72 | 33.3 | 2.57 | 26.9 | 29.14 | 33.3 | 2.26 | 29.2 | 32.49 | 40.0 | 2.22 |
| Length of lower jaw/head length | 21.3 | 25.59 | 29.2 | 1.99 | 25.0 | 27.23 | 29.6 | 1.87 | 26.7 | 30.48 | 35.0 | 2.18 |
| Width of gape/head length | 21.3 | 25.57 | 30.8 | 2.92 | 21.7 | 24.39 | 27.8 | 1.85 | 20.8 | 25.41 | 30.0 | 2.83 |
| Number of fish measured | | 15 | | | | 16 | | | | 24 | | |

Table 18. Sexual dimorphism in size and body proportions in *Galaxiella pusilla* (22 males, 21 females, Narracan Creek, Victoria).

| | | Range | Mean | S.D. |
|---|---|---|---|---|
| Size (total length — mm) | male | 24.5 - 29.5 | 27.19 | 1.24 |
| | female | 31.0 - 39.0 | 34.20 | 1.86 |
| Body depth/standard length (%) | male | 16.8 - 21.5 | 18.70 | 1.27 |
| | female | 19.0 - 23.3 | 21.09 | 0.99 |
| Pectoral-pelvic length/ standard length (%) | male | 23.7 - 29.1 | 26.06 | 1.44 |
| | female | 26.7 - 34.7 | 30.79 | 1.87 |
| Pelvic-anal length/ standard length (%) | male | 15.9 - 19.3 | 17.40 | 0.83 |
| | female | 17.0 - 22.6 | 19.00 | 1.74 |

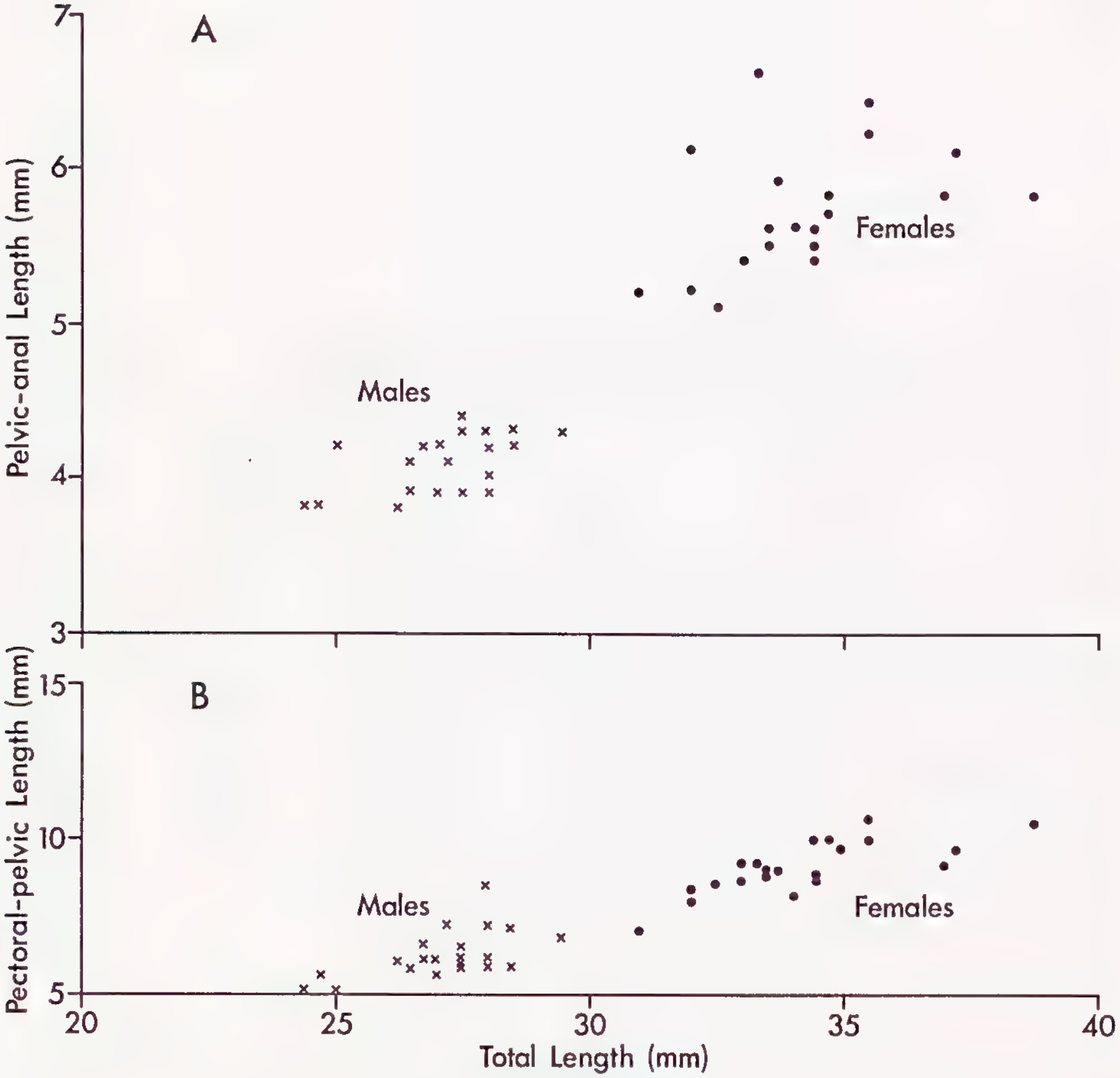

Fig. 33. Differences in body proportions between male and female *Galaxiella pusilla*.

COLOUR: The male of *G. pusilla* is characterised by a striking, narrow, orange-red stripe along its side, just below the lateral line. When alive, it is a dull olive-amber on the back and upper sides, with three black longitudinal stripes along the trunk; the upper stripe is weakest and merges medio-dorsally with darker pigment on the back. The middle stripe is much thinner and very distinct, and is positioned at about the lateral line, well-separated from the bright orange stripe along the abdomen but converging with it on the caudal peduncle. The lower dark stripe is strongly developed and forms the lower margin of the orange stripe. Ventrally there is a pair of black lines, originating together in the isthmus, diverging, and then running parallel along the belly to the pelvic fin bases; the pelvic-anal interval is more or less unpigmented but there are black lines along the anal fin base and the ventral margin of the caudal peduncle, becoming more or less confluent with the lowermost lateral dark stripe. The belly is silvery-white and the eyes silvery-gold, with small areas of bright orange, as a continuation of the lateral orange stripe.

The female differs from the male primarily in lacking the bright orange stripe. The longitudinal dark lines occur, but are a little less bold, and there is a lateral band of silvery iridescence comparable in position to the orange stripe in the female.

Juveniles lack the highly distinctive colouration, being dusky-olive on the back and sides with a silvery crenulate stripe along the lower sides.

SIZE: *G. pusilla* is a tiny species reaching a known maximum size of only 39 mm total length; it is often only 30 mm or less.

HABITAT: *G. pusilla* occurs mostly in still or gently flowing waters, usually in swamps, swampy lagoons, or small creeks and drains, mostly amongst thick aquatic vegetation.

LIFE HISTORY: Massola (1938) discussed aquarium spawning of the species which spends it entire life cycle in fresh water. He reported observations of a Mr H. W. Davey as follows: "On July 30th I noticed the male following the female about and the next day his attentions became more pressing . . . At frequent intervals of time he swam upside down before the female, but making contact with her ventral surface, rubbing himself along beneath her body, then swimming out in front of her and resuming his normal swimming position. On August 1st, egg laying commenced and continued most of the following day until I had counted 59 eggs . . . On August 5th the female died. The eyes of the embryos could easily been detected on the 11th, and on the 12th 2 eggs hatched out . . . by the 17th, 45 more had hatched out making a total of 53". Massola reported that he also had bred the species finding that the "female chooses the places to deposit the eggs" and that the "parents do not look after the eggs or young, but they don't seem to worry them either".

Further observations on the spawning of *G. pusilla* are reported by Backhouse and Vanner (1978) who have bred the species in captivity, and whose observations are in general agreement with those of Massola.

Spawning was occurring in a population in a farm drain entering Narracan Creek, near Yallourn, during August, 1977, and spawning fish were still present in the drain in October. Large numbers of larvae were present in August; spawning thus seems to occur through the spring.

*G. pusilla* is possibly able to aestivate during some life history stage. Miss J. Barclay (Department of Zoology, University of Melbourne) collected a sample from a swamp near the confluence of Diamond Creek with the Bunyip River. On returning to obtain more specimens at a later date the habitat had dried up and it was not until a further visit, after rains when water returned to the swamp, that further, mostly very small fish, were collected. These may either have invaded the area from elsewhere, or hatched from aestivating eggs. The small size of the fish caught is consistent with their having hatched recently from aestivating eggs.

DISTRIBUTION: *G. pusilla* is known in southeastern Australia, from Gippsland west to about Mount Gambier, and in northeastern Tasmania (Fig. 34).

### **Galaxiella nigrostriata** (Shipway)

Fig. 35

*Galaxias pusillus nigrostriatus* Shipway, 1953: 175 (holotype: WAM P.3420, seen; paratypes: (4) AMS IB.3197-8, seen; type locality: "a small drain running into Marbellup Creek on a property owned by Mr Byland", Elleker, near Albany, Western Australia); Munro, 1957a: 18; Gentilli, 1961: 488; Anon. 1964: 34.

*Brachygalaxias nigrostriatus* — Whitley, 1956a: 34; 1956b: 39; 1957a: 6; 1960: 29; 1964: 35; Scott, 1971a: 2.

*Galaxias nigrostriatus* — McDowall, 1973c: 197.

*Galaxiella nigrostriata* — McDowall, 1978a: 118; 1978b: 308; Lake, 1978: 27; Backhouse and Vanner, 1978: 128.

TAXONOMY: As the synonymy indicates there is some conflict of opinion about the taxonomic status of *G. nigrostriata*. Scott (1971a) suggested that full specific rank should be assigned, and this view was supported by McDowall (1978a), where the problem is discussed in detail.

DIAGNOSIS: Characterised by its small size, dorsal origin behind anal origin, absence of laterosensory pores beneath the lower jaw, and presence of two longitudinal dark stripes separated (in life) by a bright orange stripe. It differs from *G. pusilla* in characters discussed in the diagnosis of that species (p.555). It differs from *G. munda* in having more anal fin rays and fewer pelvic fin rays, shorter and fewer gill rakers, and a different arrangement of laterosensory canals on the head (Fig. 47). *G. munda* has only one dark lateral band with a very narrow pale band above it.

DESCRIPTION: A tiny stocky fusiform species, compressed behind the vent, dorsal and ventral body profiles moderately and evenly arched; body depth greatest in front of pelvic fin origin. Caudal peduncle long and deep, much longer than deep. Head short, broad and deep, a little depressed dorsally, about as broad as deep. Snout short and bluntly rounded. Mouth small, oblique, reaching back to about front of eyes; jaws equal. Eyes large, set at about upper head profile, interorbital broad and flat. Jaws without enlarged lateral canines; mesopterygoidal teeth few but strong; lingual teeth well developed. Gill rakers long and slender (Fig. 44); pyloric caeca very small, no more than two well-formed shoulders (Fig. 46). Laterosensory pores on head as in Fig. 47; no submandibular pores; eight pores in preopercular-supramaxillary series, without a distinct "dog-leg" in row below eye (fourth to seventh pores); pores in anterior nasal depression virtually separated by nostril.

Fins all small and membranous; dorsal and anal fins short-based, rounded, posterior rays extending back moderately behind fin bases. Anal fin origin distinctly in front of dorsal origin. Pectoral fins broad-based small and rounded, inserted high laterally, fin lamina distinctly vertical. Pelvic-anal interval very short, pelvic fins very small, inserted at

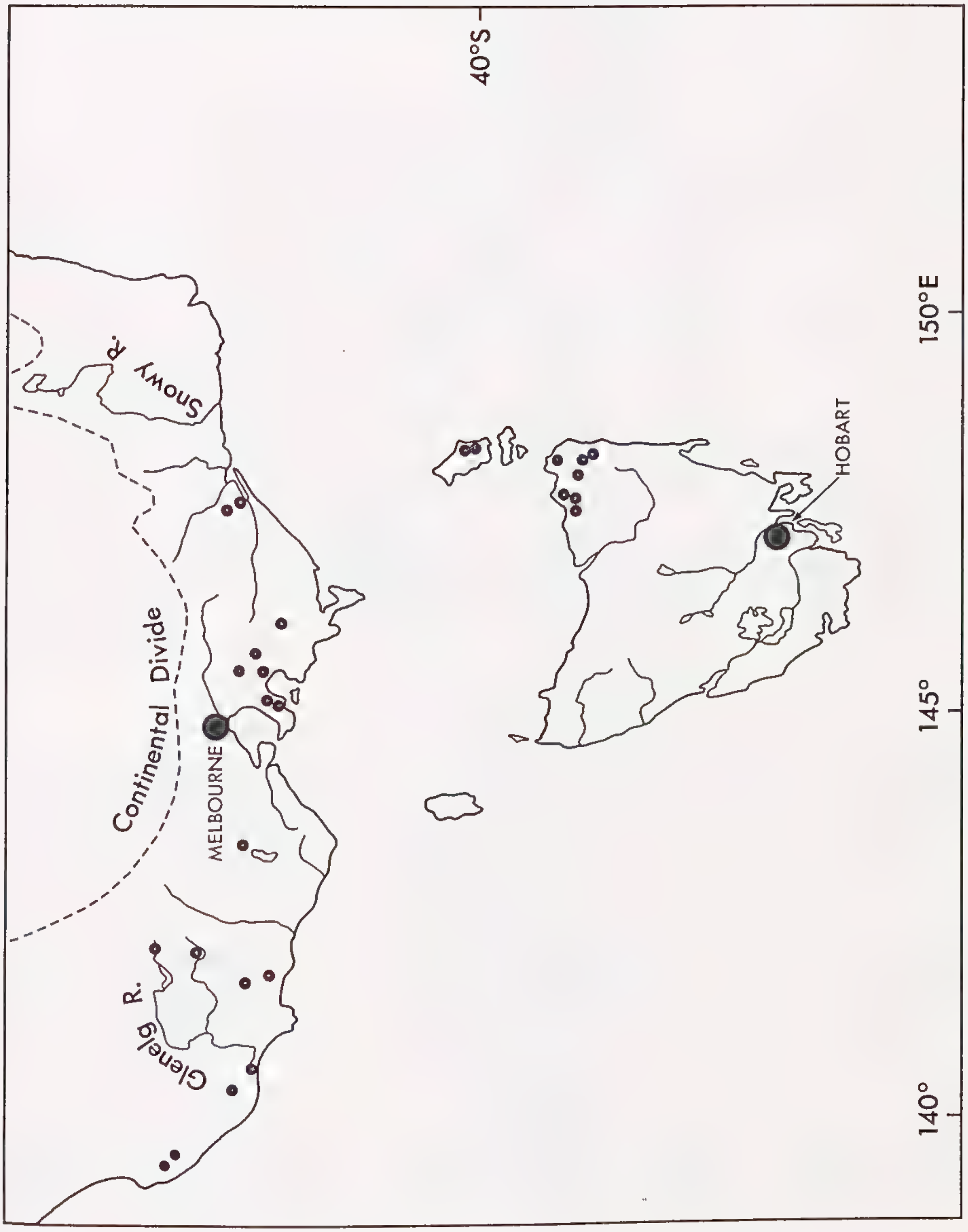

Fig. 34. Distribution of *Galaxiella pusilla*.

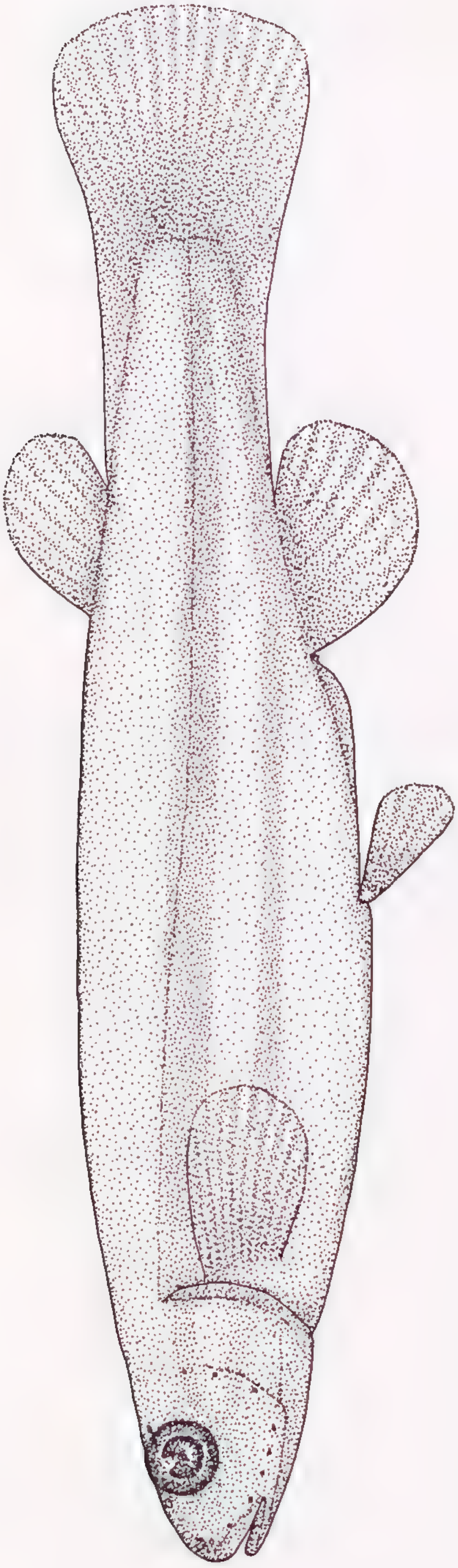

Fig. 35. *Galaxiella nigrostriata* (Shipway); swamp near Elleker, W.A., 35.5 mm T.L.

about mid-point of standard length. Caudal fin long and rounded, depth about equal to length, a little less than body depth. Caudal peduncle flanges very strongly developed and reaching forward to dorsal and anal fin bases; few procurrent caudal fin rays.

Variation: meristic; see Table 16.
morphometic: see Table 17.

COLOUR: Shipway (1953: 175) described the colour of *G. nigrostriata,* when alive, as follows: "Olivaceous above the lateral line, a black stripe below; an orange stripe below that and then another black stripe above a white ventral surface. A black spot on the dorsal portion of the posterior section of the caudal peduncle".

In preservative it is grey to brown on the back with a broad horizontal black band running mid-laterally from the mid tail-base, a little below the lateral line, across the operculum to the eye. Below this is a pale band equal in width to the darker band above, and below the pale band a second dark band, narrower than the upper one and running along the ventral surface of the caudal peduncle, along the anal fin base, and then along the lateroventral abdomen, the operculum and below the eye. The belly is unpigmented, as are all the fins. Juveniles lack the longitudinal bands.

SIZE: *G. nigrostriata* is one of the smallest galaxiids, reaching a known maximum size of only 39.5 mm total length; few specimens examined exceeded 35 mm.

HABITAT: *G. nigrostriata* is typically found in swamps, backwaters, and slow-flowing streams. Shipway (1953) collected the type series from a small drain.

LIFE HISTORY: It seem likely, from general characters of *G. nigrostriata* and from comparison with *G. pusilla,* that the life history of *G. nigrostriata* is restricted to freshwater, lacking any marine stage. The natural history of the species is unstudied.

DISTRIBUTION: *G. nigrostriata* is known only from Western Australia, where it has been colleced from streams and swamps between about Esperance and west to Albany, on the south coast (Fig. 36). In the vicinity of Albany its range overlaps that of *G. munda,* which is distributed further to the west and north.

## **Galaxiella munda** McDowall
Fig. 37

*Galaxiella munda* McDowall, 1978a: 119 (holotype: WAM P.25736-001; paratypes: (39) WAM P.5225; (5) AMS I.19522-001; type locality: pool in jarrah forest about 8 km north of Scott River, south of Canebreak Yards, between Nanup and Augusta, Western Australia, 115°29′59″ E. 34°13′50″ S.) 1978b: 308; Lake, 1978: 26; Backhouse and Vanner, 1978: 128.

TAXONOMY: Examples of this species were present among samples labelled "*Brachygalaxias nigrostriatus*" in collections in the Western Australian Museum, Perth, the National Museum of Victoria, Melbourne, the Rijksmuseum van Naturlijke Historie, Leiden, and the American Museum of Natural History, New York; although *G. munda* is better represented in collections than *G. nigrostriata,* it had escaped recognition as a distinct species.

DIAGNOSIS: Characterised by small size, the dorsal fin origin being behind the anal origin, the absence of laterosensory pores beneath the lower jaw, and the presence of a broad, dusky, longitudinal band along the lateroventral trunk (in preserved, larger adults). It closely resembles the other species of *Galaxiella* — *G. pusilla* and *G. nigrostriata* — from which it differs in characters discussed in the diagnoses of these two species (pp.555 and 562 respectively).

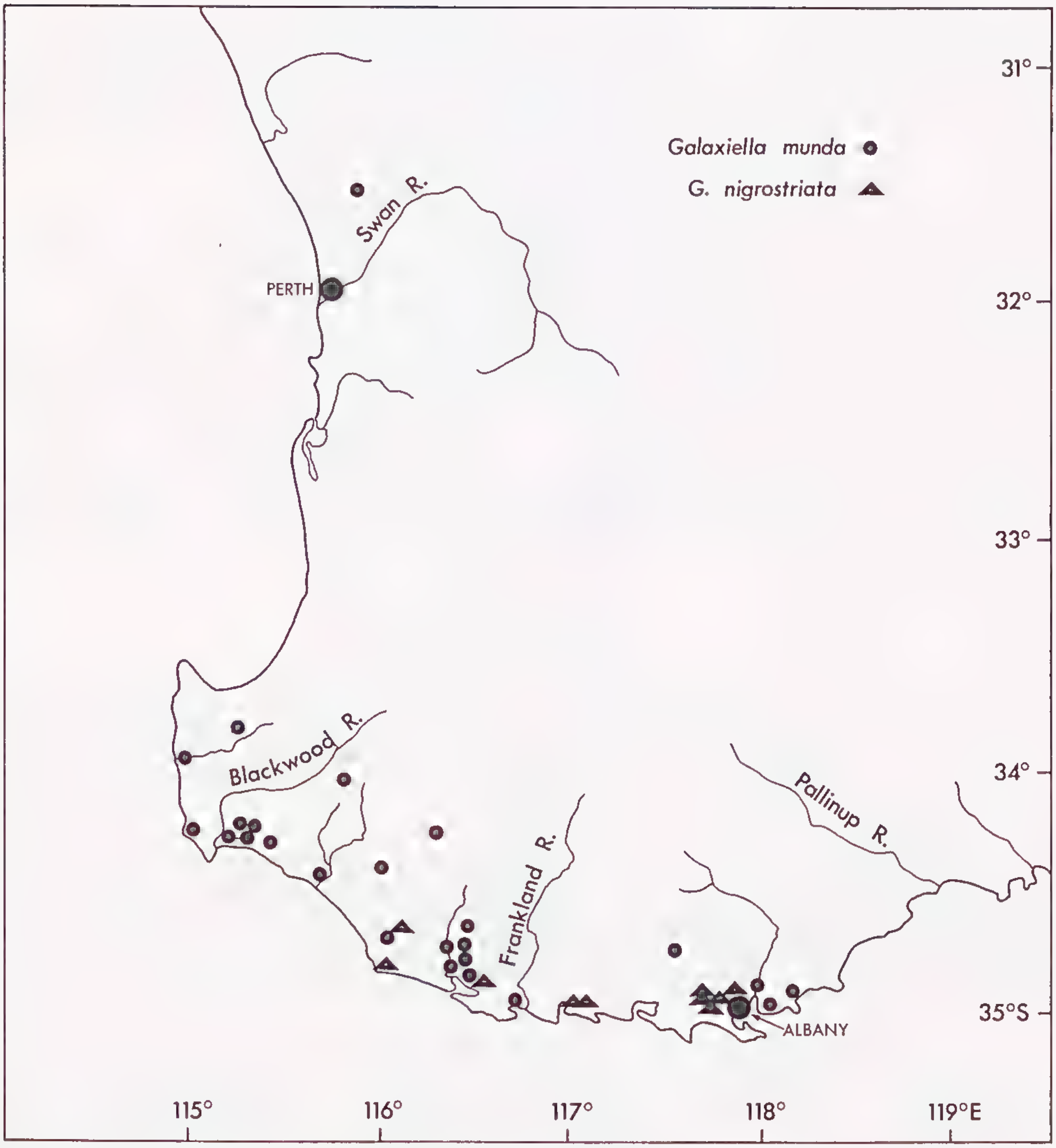

Fig. 36. Distribution of *Galaxiella nigrostriata* and *G. munda*.

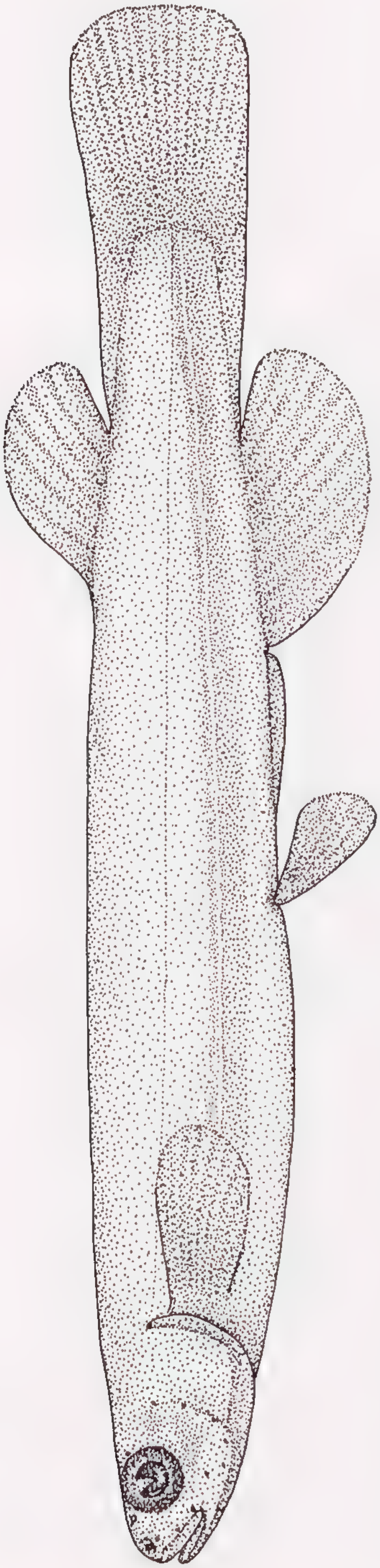

Fig. 37. *Galaxiella munda* McDowall; pool near Canebreak Yards, W.A., 45.5 mm T.L.

DESCRIPTION: A small, almost tubular species, compressed behind the vent, the dorsal and ventral body profiles almost parallel, or the belly deepened a little. Caudal peduncle long and deep, much longer than deep, head very short, of moderate depth, about as deep as broad. Snout short and bluntly rounded. Mouth small, oblique, reaching back to about front of eye, jaws about equal. Eye very large, upper margin at about head profile, interorbital broad and flat. Jaws without enlarged lateral canines; mesopterygoidal teeth few but strong; lingual teeth well developed. Gill rakers long and slender (Fig. 44); pyloric caeca lacking (Fig. 46). Laterosensory pores on head as in Fig. 47. No submandibular pores; nine pores in preopercular-supramaxillary series with a distinct "dog-leg" in row below eye (fourth to seventh pores); pores in anterior nostril depression distinctly posterior to nostril.

Fins small and membranous; dorsal fin short-based, anal much longer-based, but fins rounded and extending well back behind fin bases; posterior rays long; anal fin origin distinctly in front of dorsal origin. Pectoral fins narrow-based, small and rounded, insertion high laterally, fin lamina distinctly lateral. Pelvic-anal interval very short, pelvic fins very small, inserted at about midpoint of standard length. Caudal fin long and rounded to truncate, depth much less than length and less than body depth. Caudal peduncle flanges strongly developed and reaching forward to be more or less confluent with dorsal and anal fin bases; few procurrent caudal fin rays.

Variation: meristic: see Table 16.
morphometric: See Table 17.

COLOUR: Colour when alive variable, related to the colour of the water inhabited. In the frequently tannin-stained swampy waters of Western Australia, *G. munda* is a dark brown on the back and sides with a longitudinal crenulate, silvery stripe along the lower sides; the belly is silvery-white. Less densely coloured fish are greenish-olive on the back and upper sides with a longitudinal silvery stripe below which is a soft brownish-orange stripe and then a narrow, dark stripe. The belly is silvery.

Colour in preservative dusky grey-brown. In small fish up to about 25 mm T.L. there is general dorsal and lateral covering of melanophores, the belly unpigmented. With growth, a crenulate pale longitudinal stripe develops on the lower sides; when the fish reach about 40 mm a variously intense dark line forms above the pale stripe with a few scattered, large melanophores in the edge of the pale stripe. Below the pale line a broad, indistinct, reticulate dark band forms, below which the belly is unpigmented.

The peritoneum of the abdominal cavity is black.

SIZE: *G. munda* is by far the largest of the species of *Galaxiella* reaching a known maximum length of 52 mm T.L., not infrequently reaching 35 mm or more.

HABITAT: The habitat at the type locality was described by Mr W. H. Butler, who collected the specimens, as "A shallow, cool pool, arising out of laterite and densely covered with jarrah/marri low forest. The undergrowth tends to be *Hakea* and other sundry proteaceous bushes. The pool is quite small, approximately 2 metres long, 60 cm wide and perhaps 20 cm deep, heavily coloured with the tannin stain of *Eucalyptus* leaves". *G. munda* has been collected from the type locality of *Lepidogalaxias salamandroides* Mees (family Lepidogalaxiidae), which Mees (1961: 34) described as follows: "a very small creek in heavy forest of mixed Karri and Jarrah. The creek was on average about 30 cm wide and 5 cm deep; the creek bed was largely filled with *Eucalyptus* leaves, especially in those places where the creek was slightly wider and deeper...The creek is probably permanent, the water is cool, and fairly rapidly flowing".

Mr G. L. Liddelow of the Western Australian Forests Department collected specimens "in waterways formed by road formations" in an area described as "black peaty sands of flats subject to prolonged flooding or water-logging where there are extensive areas of sedgeland . . . with closed heath forming pockets in the wettest parts of the low, open woodland" (pers. comm.). From these accounts and from brief details on sample labels, it appears that *G. munda* occurs mostly in pools and quietly flowing streams, but that it also inhabits flowing waters.

LIFE HISTORY: Nothing is known of the life history of *G. munda;* it is most likely that its entire life cycle is spent in fresh water.

DISTRIBUTION: *G. munda* is known only from Western Australia where it is widespread in the far west and southwest, from north of Perth to the vicinity of Albany (Fig. 36). In the eastern fringes of its range it overlaps the range of *G. nigrostriata.*

## Genus **Paragalaxias** Scott

*Paragalaxias* Scott 1935 (April): 41 (type species: *Galaxias shannonensis* Scott, 1934: 41, a junior synonym of *G. dissimilis* Regan, by original designation).

*Querigalaxias* Whitley, 1935 (July): plate III (type species: *Galaxias dissimilis* Regan, 1905: 383, by original designation, genus undiagnosed).

DIAGNOSIS: Small, stocky fishes (up to 99 mm L.C.F.), trunk cylindrical to slightly compressed; scales lacking; lateral line present; open pores present on head, rows of laterosensory papillae (pit organs) on head and across tail base. Dorsal fin origin above or very slightly behind pelvic fin insertion; pelvic fins with 5-6 rays; procurrent rays numerous. No adipose fin. Vertebrae 37-44; branchiostegals 6-8. Sexes similar, both gonads present in both sexes; no pyloric caeca.

Maxilla almost excluded from gape, toothless; jaw teeth conical, uniserial, without enlarged canines laterally; mesopterygoidal teeth few and of moderate size; lingual teeth few and large. Vomer shafted but toothless; no palatine teeth. Orbitosphenoid and basisphenoid absent; ethmoid lacks dermal ossification but there is a block of endochondral bone including an ethmomyodomal. Post-temporal simple; no mesocoracoid; postcleithrum present. Epineurals and epipleurals present. Five hypurals plus a parhypural on urostylar centrum; caudal neural and haemal spines compressed caudally.

Four species in the highlands of central Tasmania. (Identification of *Galaxias dissimilis* Regan with one of the species in Great Lake, Tasmania, suggests that the type locality for this species, 'New South Wales' is incorrect. Certainly no further specimens identifiable with *G. dissimilis* have been found in continental Australia).

Stokell's (1950) inclusion of the South African species *G. zebratus* (Castelnau) has been shown elsewhere to be erroneous (Scott 1966; McDowall 1973b).

## KEY TO SPECIES OF *PARAGALAXIAS*

1. Gill rakers 9-10 (occasionally up to 12); caudal rays 14(13); vertebrae 37-39(40); no submandibular pores (Great Lake and Shannon Lagoon, Tasmania) .......................................................................................... *P. eleotroides* p.575.
   Gill rakers 12-18; caudal rays 15(14); vertebrae 40-42(44); submandibular pores present or absent. ..........................................................................................2

2. Pelvic rays 5; gill rakers very short stubs, length about equal to basal width; anterior interorbital laterosensory pore well-separated from posterior nostril

(Julian Lakes, Ida and Tallinah Lagoons, and Lakes Dudley, and Ada, Tasmania). ..............................................................................................*P. julianus,* p.581.
Pelvic rays 6; gill rakers longer, length much greater than basal width; anterior interorbital laterosensory pore confluent with posterior nostril..........................3

3. Dorsal rays 9-12; gill rakers 12-15; vertebrae 40-41; two pairs of submandibular pores, widely separate; supramaxillary pores very large (Great Lake, Shannon Lagoon and Penstock Lagoon, Tasmania) ..............................*P. dissimilis,* p.570.
Dorsal rays 13-14; gill rakers 16-18 (occasionally 15); vertebrae 42-43 (occasionally 41 or 44); submandibular pores rarely present, if present close together; supramaxillary pores small (Arthurs Lake and Woods Lake, Tasmania) ........................................................................*P. mesotes,* p.578.

### **Paragalaxias dissimilis** (Regan)

Fig. 38

*Galaxias dissimilis* Regan, 1905: 383 (holotype: BMHN 1905.7.29:1, not seen; type locality: "New South Wales", probably erroneous); McCulloch, 1921: 28; 1922: 18; 1929: 49; Whitley, 1933: 61; Scott, 1935: 46; 1936: 110; Frankenberg, 1966b: 27; Scott, 1966: 248; 1971a: 8.

*Paragalaxias shannonensis* Scott, 1935: 41 (holotype: formerly QVML HT 939a, now lost — Andrews, 1976; paratypes: (1) QVML PT 939b, seen; (1) BMNH 1935.10.19:2, not seen; (1) AMS IA.6439, seen; (1) NMVM A.413, seen; (2) TMH D.996, D.1/180, seen; type locality: Shannon River, Tasmania); Whitley, 1935: 42; Scott, 1936: 110; 1941: 60; Stokell, 1945: 128; 1950: 2; 1953: 20; Whitley, 1956a: 34; Munro, 1957b: 15; Scott, 1966: 247; Frankenberg, 1966a: 162; 1966b: 28; 1966c: 22; Lynch, 1966: 14; 1967: 20; Dixon, 1972: 121; McDowall, 1973b: 94; Andrews, 1973: 105; Lake, 1971: 20; Lynch, 1974: 15; Green, 1974: 3; Frankenberg, 1974: 123; Lake, 1974: 449; Andrews, 1976: 331 *(partim).*

*Querigalaxias dissimilis* — Whitley, 1935: plate III.

*Paragalaxias dissimilis* — Stokell, 1950: 2; 1953: 50; Whitley, 1956a: 34; 1956b: 39; 1957a: 6; Munro, 1957b: 15; Whitley, 1964: 35; Lake, 1971: 20; McDowall, 1973b: 94; McDowall and Fulton, 1978a: 95; 1978b: 664; Lake, 1978: 26.

TAXONOMY: Stokell (1950) first proposed that *P. shannonensis* is a junior synonym of *P. dissimilis,* but Scott (1966) rejected this, suggesting, in particular, that the dorsal fin is in front of the pelvic fins in *P. dissimilis* but behind in *P. shannonensis*. Study of material identifiable with *P. shannonensis* from Great Lake, Tasmania, indicates that Stokell is probably correct, and we follow Stokell (1950) in regarding *P. shannonensis* as a junior synonym of *P. dissimilis* (see McDowall and Fulton, 1978a).

DIAGNOSIS: Characterised by large dorsal fin above pelvic fins, very large laterosensory pores on head, and long gill rakers. The large pores and long rakers distinguishing it from all other species of *Paragalaxias.*

Differs from *P. eleotroides* in having a somewhat shorter and more forked tail (S.L./T.L. ratio higher), a higher predorsal/preanal ratio, a shorter-based dorsal fin, a broader interorbital (Table 20), and in having 15 principal caudal rays, more and longer gill rakers, and more vertebrae (Table 19). There are two pores on each side below the lower jaw (submandibular) in *P. dissimilis,* none in *P. eleotroides* (Fig. 47).

Differs from *P. mesotes* in having a longer dorsal fin base, larger pectoral fins (Table 20), and in having more dorsal fin rays, gill rakers, and vertebrae (Table 19). *P. dissimilis* regularly has two, large, well-separated submandibular laterosensory pores,

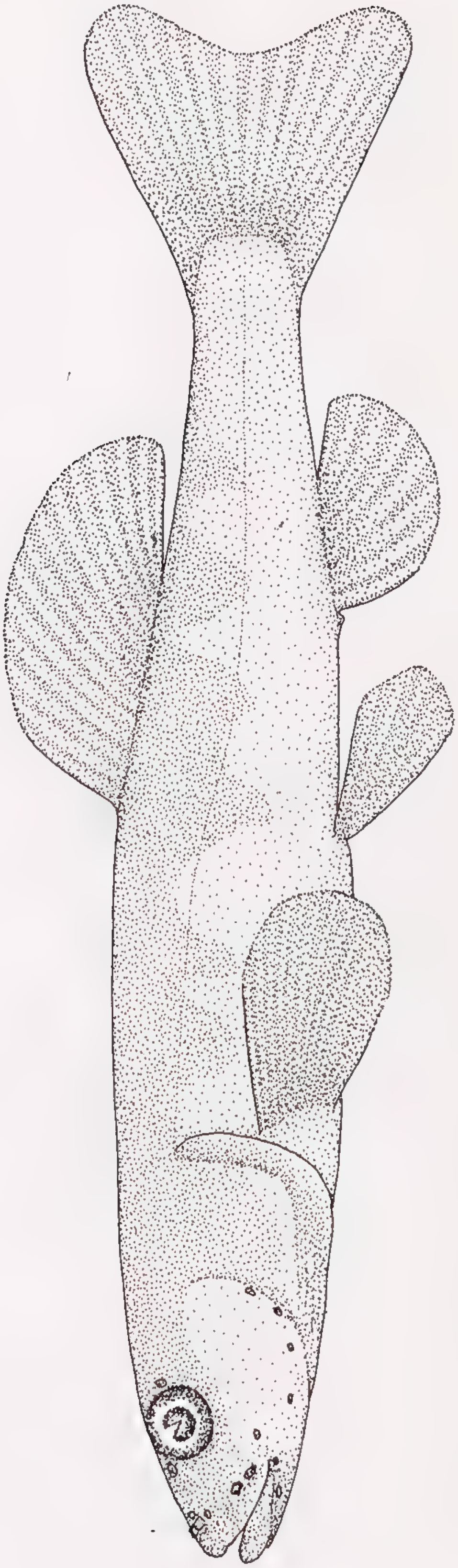

Fig. 38. *Paragalaxias dissimilis* (Regan); Great Lake, Tas. 57 mm L.C.F.

while *P. mesotes* usually lacks such pores — if present they are small and close together.

Differs from *P. julianus* in having a much longer dorsal fin base, much bigger pectoral and pelvic fins, a longer head (Table 20), and in having more dorsal fin rays, pelvic fin rays and gill rakers (Table 19). In *P. dissimilis* the opening of the anterior interorbital laterosensory pores is confluent with the posterior nostril but in *P. julianus* the two openings are well separated (Fig. 47).

DESCRIPTION: A small, stout, bullet-shaped species, the trunk rounded in section, the back and belly moderately and evenly arched; depressed anteriorly on head, and somewhat compressed behind vent. Caudal peduncle long and slender, much longer than deep. Head long, flattened, about as broad as deep. Snout long, broad and flattened. Mouth large, moderately oblique, extending back to or a little beyond anterior eye margin; jaws about equal in length. Eyes of moderate size with upper margin at about head profile, inter-orbital broad and flat. Jaws without enlarged canine teeth. Gill rakers long and slender (Fig. 44). Pyloric caeca lacking (Fig. 46).

Open pores on head very large, particularly those above upper jaw. Disposition of pores as shown in Fig. 47. Only four pores in preopercular series; opening of pore adjacent to posterior nostril with a visible partition between pore and nostril; two well-separated sub-mandibular pores.

Fins well developed. Some thickening at bases of dorsal and anal fins. Dorsal fin inserted at about pelvic fin origin, distinctly behind midpoint of standard length, fin high and quite long-based, and extending well back behind fin base; anal fin much smaller, short-based, origin below rear of dorsal fin. Pectoral fins large, inserted low lateroventrally. Pelvic fins also quite large, inserted distinctly behind midpoint of standard length. Caudal fin forked, fin lobes rounded, fin depth about equal to body depth; peduncle flanges well developed but not extending far forward on caudal peduncle.

Variation: meristic: see Table 19;
morphometric: see Table 20.

COLOUR: Colour in life highly variable and relating to substrate colour; often very dark green-grey to almost black, varying to olive-brownish. The sides are traversed by indistinct to quite bold grey-black blotches which are confluent with the darker colouration of back. There is olive-gold iridescence on the opercula and belly and the eyes are golden. The fins are olive coloured and unmarked.

In preservative a dull grey-black on the top and sides of the head and on the back, this darker colour extending down on to the sides as broad bands which alternate with the paler grey of the lower sides and belly, or often about six dark grey oval spots or blotches.

SIZE: *P. dissimilis* was described from a holotype 75 mm L.C.F. (65 mm S.L.); no further examples this large are known; the largest seen in this study was 72 mm L.C.F. (62 mm S.L.); the species commonly exceeds 50 mm L.C.F.

NATURAL HISTORY: *P. dissimilis* is a lacustrine species, and is not known in streams flowing into lakes except for some taken at the edge of a short section of stream connecting Great Lake and Shannon Lagoon (Scott, 1935). It is usually found amongst rocks around the margins of lakes, often in only a few centimetres of water; however, it may be taken from amongst both dead and living vegetation and beneath planks, sheets of iron and from inside cans. Small examples have been taken in dredge samples at

Table 19. Meristic variation in *Paragalaxias* species.

| | | *P. dissimilis* | *P. eleotroides* | *P. mesotes* | *P. julianus* |
|---|---|---|---|---|---|
| Dorsal rays — segmented | 9 | | | 1 | 3 |
| | 10 | | | 6 | 15 |
| | 11 | | | 10 | 2 |
| | 12 | | 1 | 6 | |
| | 13 | 17 | 12 | | |
| | 14 | 9 | 7 | | |
| total | 10 | | | 1 | 4 |
| | 11 | | | 5 | 14 |
| | 12 | | | 11 | 2 |
| | 13 | | 1 | 6 | |
| | 14 | 11 | 11 | | |
| | 15 | 9 | 7 | | |
| | 16 | | 1 | | |
| Anal rays — segmented | 6 | | 3 | | |
| | 7 | 1 | 16 | 3 | 12 |
| | 8 | 13 | 1 | 18 | 8 |
| | 9 | 7 | | 2 | |
| total | 7 | | 3 | | 1 |
| | 8 | 1 | 16 | 3 | 13 |
| | 9 | 12 | 1 | 18 | 6 |
| | 10 | 7 | | 2 | |
| Caudal rays — principal | 13 | | 1 | | |
| | 14 | 1 | 19 | | 1 |
| | 15 | 20 | | 23 | 19 |
| Pectoral rays | 11 | | | | 1 |
| | 12 | 1 | | | 4 |
| | 13 | 15 | 11 | 4 | 10 |
| | 14 | 5 | 9 | 15 | 5 |
| | 15 | | | 5 | |
| Pelvic rays | 5 | | 1 | | 20 |
| | 6 | 21 | 19 | 23 | |
| Vertebrae | 37 | | 3 | | |
| | 38 | | 19 | | |
| | 39 | | 2 | | |
| | 40 | | 1 | 9 | 2 |
| | 41 | 3 | | 14 | 15 |
| | 42 | 34 | | | 12 |
| | 43 | 10 | | | 3 |
| | 44 | 1 | | | |
| Gill rakers | 9 | | 10 | | |
| | 10 | | 9 | | |
| | 11 | | 0 | | |
| | 12 | | 1 | 3 | 6 |
| | 13 | | | 7 | 9 |
| | 14 | | | 10 | 4 |
| | 15 | 1 | | 3 | 1 |
| | 16 | 9 | | | |
| | 17 | 12 | | | |
| | 18 | 3 | | | |

Table 20. Morphometric variation in *Paragalaxias* species. Figures are given as percentages of denominator in ratios.

| | *P. dissimilis* | | | | *P. mesotes* | | | | *P. eleotroides* | | | | *P. julianus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Min. | Mean | Max. | S.D. | Min. | Mean | Max. | S.D. | Min. | Mean | Max. | S.D. | Min. | Mean | Max. | S.D. |
| Standard length/Total length | 85.6 | 87.25 | 89.7 | 1.16 | 87.1 | 88.64 | 90.9 | 1.24 | 82.1 | 84.63 | 86.8 | 1.13 | 87.2 | 88.52 | 90.5 | 1.07 |
| Body length at vent/Standard length | 12.8 | 13.89 | 15.2 | 0.58 | 12.5 | 13.62 | 14.8 | 0.63 | 11.9 | 13.25 | 14.4 | 0.66 | 11.6 | 12.81 | 13.9 | 0.66 |
| Length of caudal peduncle/Standard length | 18.4 | 19.62 | 21.4 | 0.78 | 17.2 | 18.72 | 20.7 | 1.00 | 18.5 | 20.67 | 23.1 | 1.12 | 19.2 | 20.93 | 22.2 | 0.89 |
| Depth of caudal peduncle/Length of peduncle | 43.7 | 48.41 | 54.1 | 2.81 | 38.2 | 48.31 | 55.0 | 3.61 | 39.4 | 45.24 | 52.2 | 3.42 | 40.0 | 44.90 | 50.0 | 2.62 |
| Predorsal length/Standard length | 55.7 | 57.56 | 59.5 | 1.04 | 58.0 | 59.60 | 61.6 | 0.91 | 53.5 | 55.07 | 57.0 | 1.04 | 57.5 | 58.74 | 60.9 | 0.89 |
| Predorsal length/Pre anal length | 78.2 | 80.32 | 83.9 | 1.47 | 79.7 | 81.84 | 84.6 | 1.41 | 75.5 | 77.58 | 81.7 | 1.94 | 78.9 | 80.85 | 83.3 | 1.10 |
| Length of dorsal fin base/ Standard length | 18.0 | 19.37 | 20.7 | 0.82 | 12.9 | 14.84 | 17.8 | 1.12 | 19.6 | 23.10 | 25.4 | 1.46 | 12.3 | 14.48 | 16.4 | 1.17 |
| Maximum length of dorsal fin/ Basal length | 135.3 | 143.82 | 153.3 | 4.79 | 132.1 | 151.01 | 170.0 | 9.83 | 122.2 | 134.87 | 158.6 | 7.84 | 131.0 | 136.69 | 147.8 | 7.26 |
| Length of anal fin base/ Standard length | 7.9 | 9.98 | 11.7 | 0.96 | 8.6 | 9.67 | 10.7 | 0.65 | 8.2 | 9.57 | 12.0 | 1.06 | 8.4 | 9.42 | 10.7 | 0.76 |
| Maximum length of anal/ Basal length | 161.1 | 180.87 | 201.1 | 14.02 | 150.0 | 165.42 | 185.7 | 7.71 | 153.3 | 187.3 | 218.2 | 19.36 | 138.9 | 154.64 | 171.4 | 10.21 |
| Pectoral fin length/ Pectoral-pelvic length | 77.4 | 72.93 | 100.0 | 6.53 | 56.4 | 64.90 | 76.7 | 6.75 | 60.9 | 77.26 | 92.1 | 7.25 | 48.4 | 57.00 | 66.7 | 5.19 |
| Pelvic fin length/Pelvic-anal length | 60.9 | 88.00 | 91.8 | 5.64 | 63.8 | 75.35 | 88.5 | 7.40 | 67.7 | 81.13 | 88.9 | 6.35 | 57.1 | 67.05 | 82.8 | 7.57 |
| Pre pelvic length/Standard length | 54.2 | 56.77 | 59.0 | 1.24 | 54.9 | 56.49 | 58.7 | 1.07 | 52.3 | 53.95 | 56.2 | 1.24 | 53.6 | 55.97 | 57.6 | 1.05 |
| Pectoral-pelvic length/ Standard length | 25.6 | 27.61 | 30.5 | 1.40 | 25.0 | 28.11 | 30.2 | 1.39 | 25.7 | 28.06 | 31.6 | 1.47 | 28.0 | 29.65 | 32.5 | 1.22 |
| Pelvic-anal length/Standard length | 14.6 | 16.68 | 18.5 | 0.94 | 15.6 | 18.02 | 19.8 | 1.13 | 17.8 | 19.06 | 20.3 | 8.68 | 16.3 | 18.21 | 19.4 | 0.86 |
| Head length/Standard length | 29.5 | 30.57 | 32.0 | 0.72 | 28.2 | 29.96 | 31.8 | 0.88 | 25.3 | 27.93 | 30.0 | 1.27 | 27.2 | 28.67 | 29.8 | 0.77 |
| Head width/Head length | 50.0 | 52.84 | 59.3 | 2.92 | 53.1 | 56.41 | 62.3 | 2.33 | 52.9 | 58.79 | 68.8 | 3.94 | 55.7 | 59.92 | 63.2 | 2.55 |
| Head depth/Head length | 48.0 | 52.31 | 57.4 | 2.74 | 46.6 | 52.31 | 56.1 | 2.64 | 52.9 | 57.95 | 65.0 | 3.09 | 50.0 | 53.97 | 58.8 | 2.43 |
| Snout length/Head length | 30.6 | 33.48 | 37.1 | 1.70 | 28.6 | 31.90 | 34.7 | 1.42 | 31.4 | 33.76 | 37.5 | 1.56 | 31.6 | 34.57 | 37.5 | 1.47 |
| Post orbital head length/Head length | 48.3 | 52.08 | 57.4 | 2.64 | 50.0 | 53.79 | 60.0 | 2.69 | 50.0 | 55.26 | 60.00 | 3.11 | 50.0 | 53.04 | 58.0 | 2.21 |
| Inter orbital width/Head length | 28.0 | 31.10 | 35.2 | 1.91 | 28.8 | 31.86 | 36.4 | 1.98 | 23.5 | 27.52 | 31.6 | 2.97 | 30.1 | 33.81 | 36.6 | 2.03 |
| Eye diameter/Head length | 19.0 | 21.61 | 24.1 | 1.50 | 17.6 | 21.46 | 25.5 | 1.77 | 20.0 | 22.93 | 25.6 | 1.51 | 16.7 | 19.51 | 22.0 | 1.87 |
| Length of upper jaw/Head length | 35.9 | 38.01 | 41.1 | 1.63 | 33.3 | 36.67 | 39.7 | 1.68 | 28.2 | 34.88 | 39.6 | 2.60 | 34.4 | 37.10 | 40.0 | 1.67 |
| Length of lower jaw/Head length | 31.5 | 34.97 | 38.8 | 1.89 | 31.3 | 34.70 | 38.2 | 1.74 | 28.2 | 33.23 | 39.6 | 2.85 | 33.0 | 35.78 | 39.4 | 1.76 |
| Width of gape/Head length | 28.0 | 32.34 | 37.0 | 2.63 | 28.6 | 32.75 | 34.8 | 1.76 | 28.2 | 32.39 | 38.1 | 3.63 | 32.9 | 36.13 | 39.1 | 2.08 |
| Number of fish measured | | 20 | | | | 23 | | | | 20 | | | | 20 | | |

depths of up to 10 m. Although it is a common species it is secretive during the day and is therefore seldom seen. When placed in an aquarium it is an active, mid-water swimming species and does not rest on the bottom as does *P. eleotroides*. It seems likely that it is most active during the night.

DISTRIBUTION: *P. dissimilis* is confined to the Central Plateau region of Tasmania, having been collected from Great Lake, Shannon Lagoon, the Shannon River connecting these two bodies of water, and Penstock Lagoon. The two lagoons are artificial impoundments downstream from Great Lake (Fig. 39).

### **Paragalaxias eleotroides** McDowall and Fulton

Fig. 40

*Paragalaxias shannonensis* — Stokell, 1950: 3; Scott 1966: 247; Andrews, 1976: 332 (*partim* — non *Paragalaxias shannonensis* Scott, 1935: 41, a junior synonym of *P. dissimilis* (Regan, 1905: 383)).

*Paragalaxias eleotroides* — McDowall and Fulton, 1978a: 101 (holotype: TMH D.1259, seen; paratypes: (2) TMH D. 1261-2, seen; (2) QVML 1976.5.166 (type 213), seen; (6) AMS I. 19152-001, seen; (2) BMNH 1976.8.13:6-7, seen; type locality: shallow water along the shore of Swan Bay, Great Lake, Tasmania); 1978b: 664; Lake, 1978: 27.

TAXONOMY: The wide range of vertebral counts published by Stokell (1950) — viz. 37-44 — indicates that his samples contained both *P. dissimilis* and *P. eleotroides*. Andrews (1976) appears to have described only *P. dissimilis*, but figured *P. eleotroides*.

DIAGNOSIS: Characterised by dorsal fin above pelvic fins, stocky build, blunt head and steep snout profile, and truncate caudal fin.

Differs from *P. dissimilis* in characters discussed in the diagnosis of that species (p.570).

Differs from *P. mesotes* in having a longer and less forked tail (S.L./T.L. ratio higher), lower predorsal/S.L. and predorsal/preanal ratios, a much longer-based dorsal fin, somewhat larger pectoral and pelvic fins, a narrower interorbital (Table 20), and also in having only 14 principal caudal fin rays, fewer anal rays, gill rakers and vertebrae (Table 19); the gill rakers are much shorter in *P. eleotroides*.

Differs from *P. julianus* in having a much longer dorsal fin base, much larger pectoral and pelvic fins, a narrower interorbital and smaller eye (Table 20); also in having fewer dorsal fin rays, caudal fin rays and vertebrae, and more pelvic fin rays and gill rakers (Table 19). Whereas *P. eleotroides* has no submandibular laterosensory pores and has the anterior interorbital pore confluent with the posterior nostril, in *P. julianus* there are two pairs of submandibular pores, and the anterior interorbital pore is well separated from the posterior nostril.

DESCRIPTION: A small, stout-bodied species, the trunk rounded in section, the belly rather flattened and the back more arched; depressed anteriorly on head and somewhat compressed behind vent. Caudal peduncle long and slender, much longer then deep. Head of moderate length, somewhat flattened ventrally, profile of snout moderately steep, snout blunt, cheeks broadening a little below eyes. Mouth scarcely oblique, of moderate size, extending back to about front of eyes, jaws about equal. Eyes moderate, upper margin at head profile, interorbital of moderate width, flat. Jaws without enlarged canines; gill rakers very short and stout (Fig. 44). Pyloric caeca lacking (Fig. 46). Open pores on head small; disposition as shown in Fig. 47. Five pores in

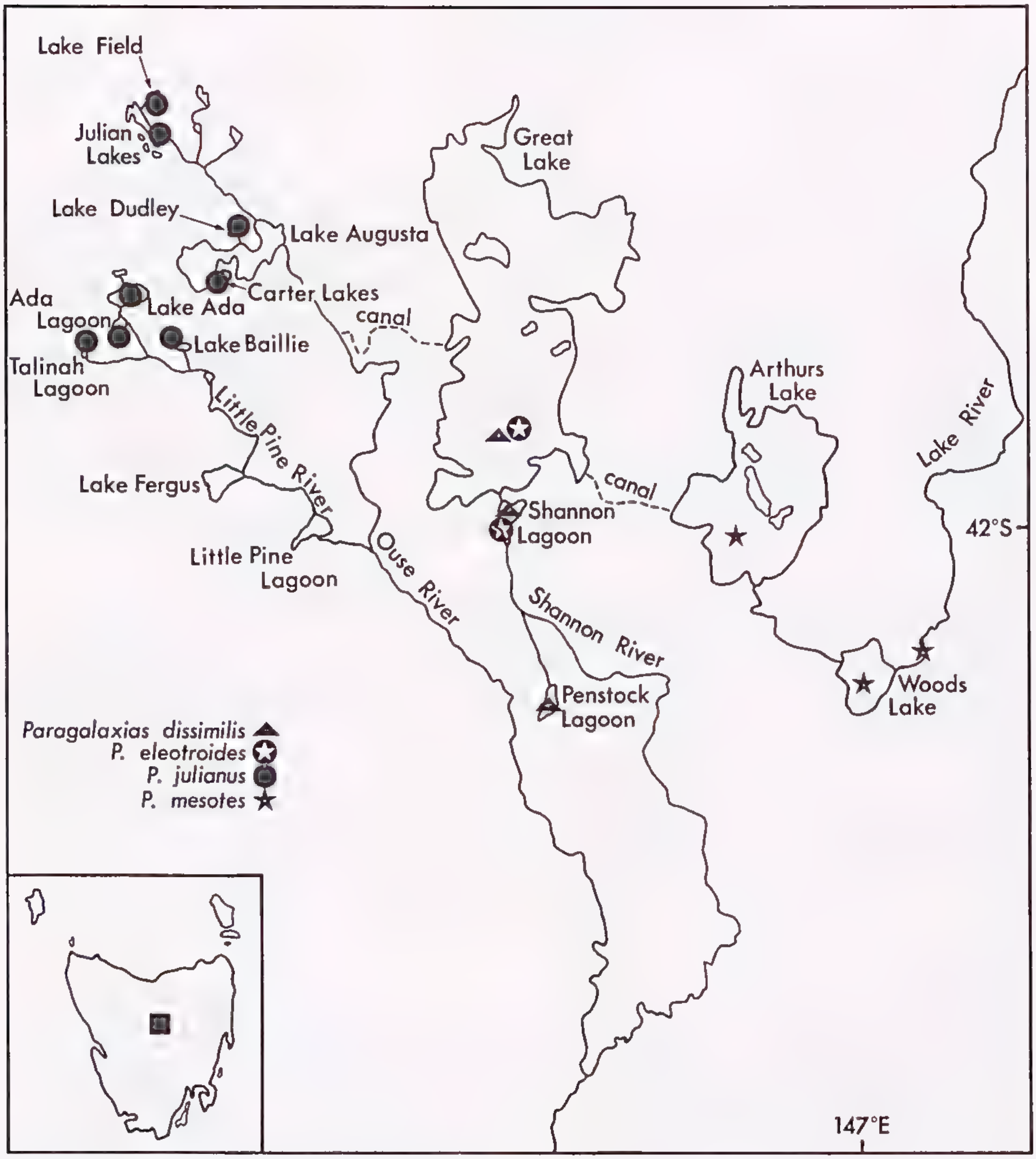

Fig. 39. Distribution of *Paragalaxias* species.

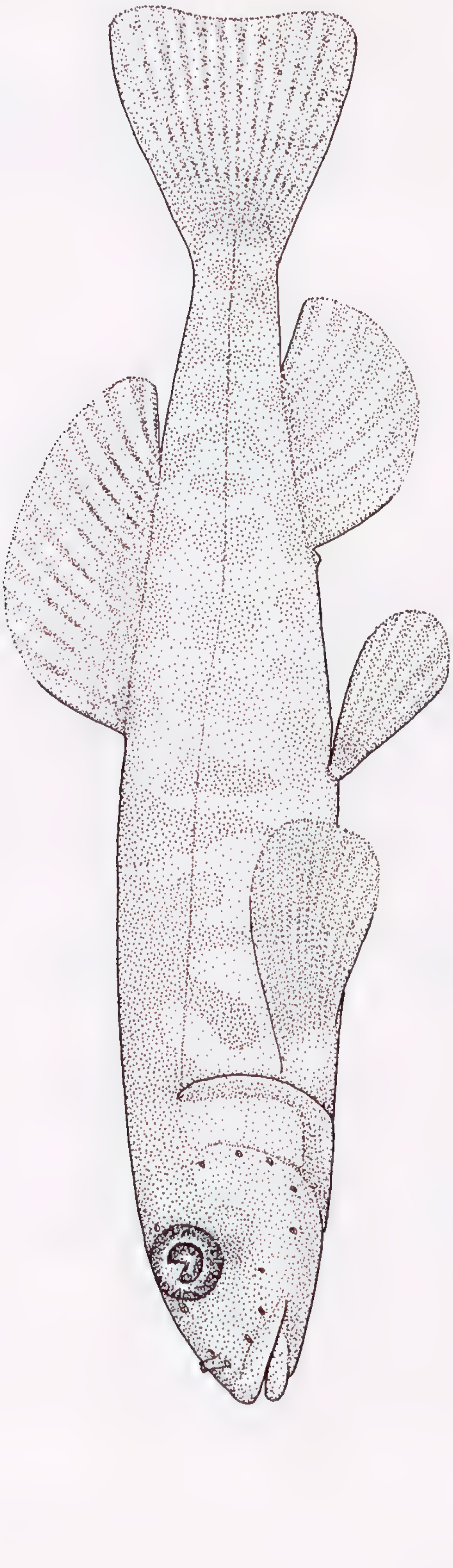

Fig. 40. *Paragalaxias eleotroides* McDowall and Fulton; Great Lake, Tas. 50 mm L.C.F.

preopercular series; opening of pore adjacent to posterior nostril without a visible partition between pore and nostril; no submandibular pores.

Fins well developed, little basal thickening. Dorsal fin inserted at about pelvic fin bases, distinctly behind mid-point of standard length, fin long-based, moderately high and rounded, and extending somewhat back beyond fin base; anal fin much smaller than dorsal, origin below rear of dorsal. Pectoral fins large, inserted low lateroventrally; pelvic fins also quite large, inserted distinctly behind mid-point of standard length. Caudal fin truncate to emarginate, fin tips rounded, fin depth less than body depth; peduncle flanges weak.

Variation: meristic: see Table 19.
morphometric: see Table 20.

COLOUR: Colour in life light brown-gold with no obvious bands, but irregular and diffuse blotching and speckling on sides and over back. Eye golden. Fins amber to olive with quite distinct black blotches along fin rays.

In preservative the fish are contrasting dark grey and pale grey-white, the back with dark patches, these spreading on to the sides as smaller and more fragmented patches, with a tendency for there to be a mid-lateral series of dark patches. The belly is greyish-white.

SIZE: *P. eleotroides* is a small species reaching only 59 mm T.L. (51 mm S.L.); it commonly reaches 40 mm T.L.

NATURAL HISTORY: *P. eleotroides* was collected from shallow water at the rocky margins of Great Lake, which seems to be its favoured habitat; it was also taken from amongst marginal aquatic vegetation and dead terrestrial scrub inundated by a rise in lake level, beneath planks, sheets of iron and from inside cans, as well as in dredge samples from depths of up to 10 m. It is secretive in habit and is seldom seen. As the name of the species implies there are similarities to eleotrids, both in general appearance, the darting, benthic habits, and also the habit of remaining at rest on the bottom with the anterior part of the body slightly elevated and supported by the pectoral fins (c.f. pelvic fins in eleotrids). When placed in an aquarium it remains on or close to the bottom at nearly all times.

DISTRIBUTION: *P. eleotroides* has restricted distribution in the Central Plateau of Tasmania, at present being known only from Great Lake and Shannon Lagoon (Fig. 39).

### **Paragalaxias mesotes** McDowall and Fulton
Fig. 41

*Paragalaxias shannonensis* — Scott, 1966: 247; Andrews, 1976: 332 (*partim* — non *Paragalaxias shannonensis* Scott, 1935: 41, a junior sysnonym of *P. dissimilis* (Regan, 1905: 383) ).

*Paragalaxias mesotes* McDowall and Fulton, 1978a: 103 (holotype: TMH D.1260, seen; paratypes: (3) TMH D.1263-5, seen; (3) QVML 1976/5/167 (type 214), seen; (6) AMS I.19151-001; seen; (2) BMNH 1976.8.13:4-5, seen; type locality: amongst rocks around the shore near pumping station at Arthurs Lake, Tasmania); 1978b: 664; Lake, 1978: 28.

DIAGNOSIS: Characterised by bullet-shaped form, smallish dorsal fin above pelvic fins, and bold coloration.

Differs from *P. dissimilis* and *P. eleotroides* in features discussed in diagnoses of these two species (pp.570 and 575 respectively).

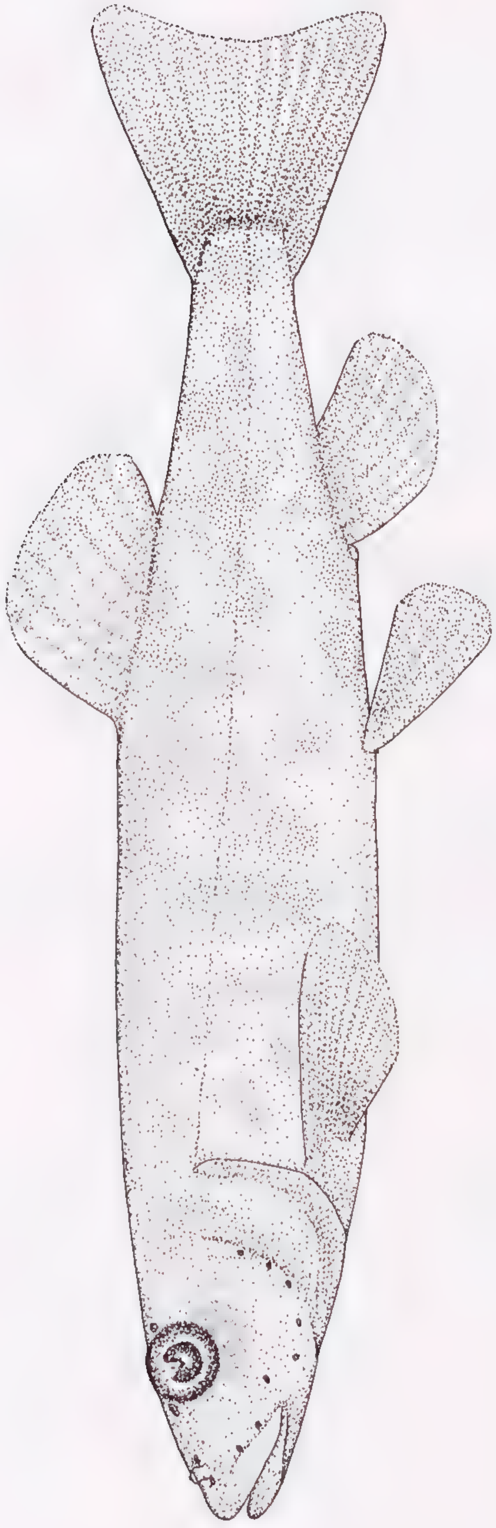

Fig. 41. *Paragalaxias mesotes* McDowall and Fulton; Arthurs Lake, Tas. 66.5 mm L.C.F.

Differs from *P. julianus* in having much longer gill rakers, in usually lacking submandibular laterosensory pores, and in having the opening of the anterior interorbital pores confluent with the posterior nostril (pore and nostril well separated in *P. julianus*).

DESCRIPTION: A small, stout species, the trunk rounded in section, somewhat flattened ventrally, the back more arched; depressed anteriorly on head, compressed behind vent. Caudal peduncle long and slender, length much greater than depth. Head long, ventrally flattened, dorsal profile sloping to a blunt point. Snout long. Mouth large, slightly oblique, extending back to or a little beyond anterior eye margin, jaws about equal in length. Eyes of moderate size, upper margins at head profile or projecting slightly above, interorbital flat to slightly concave. Jaws without enlarged canine teeth. Gill rakers moderately long, slender (Fig. 44); pyloric caeca lacking (Fig. 46).

Open pores on head small; disposition as shown in Fig. 47, somewhat variable, particularly the series above and below jaws. Five pores in preopercular series; opening of pore adjacent to posterior nostril with a visible partition between pore and nostril; usually no submandibular pores, but irregularly on one side or both there may be one pore, or two closely adjacent pores.

Fins well developed. Dorsal fin inserted somewhat behind pelvic fin bases and distinctly behind mid-point of standard length; fin rounded and short-based, and extending back well beyond fin base; anal fin much smaller, originating below rear of dorsal fin. Pectoral fins of moderate size, insertion low lateroventrally. Pelvic fins also of moderate size, inserted distinctly behind mid-point of standard length. Caudal fin slightly forked to emarginate, fin tips rounded, fin depth somewhat less than body depth; peduncle flanges well developed but not extending far forwards on caudal peduncle.

Variation: meristic: see Table 19.
morphometric: see Table 20.

COLOUR: Colour in life very bold dark greenish-grey on the back, this colour spreading down sides as irregular bands that become fragmented into isolated patches; paler trunk colour grey to olive-gold, belly silvery-grey; head olive-grey and eyes golden; fins amber with some darker colouration along the fin rays.

In preservative very boldly contrasting grey and creamish white; smaller specimens have more irregular and fragmented markings closely resembling *P. eleotroides*.

SIZE: *P. mesotes* reaches a known length of 73 mm L.C.F. (65 mm S.L.) and not uncommonly exceeds 60 mm L.C.F.

NATURAL HISTORY: *P. mesotes* in Arthurs Lake is much less common than the species of *Paragalaxias* in Great Lake. It has been collected mostly from the cover of man-made rock piles at construction sites; it was taken rarely from amongst aquatic weeds which bordered the rocky areas, although it seems likely that it would move into these areas to feed, perhaps at night. It was not collected from streams entering the lakes, although two small specimens were taken from the upper part of Lake River at a time when the river was not flowing.

DISTRIBUTION: *P. mesotes* is known only from the eastern part of the Central Plateau of Tasmania, from Arthurs Lake, Woods Lake and the Lake River below the Woods Lake dam (Fig. 39).

### **Paragalaxias julianus** McDowall and Fulton
Fig. 42

*Paragalaxias julianus* McDowall and Fulton 1978b: 660 (holotype: TMH D.1327, seen; paratypes: (4) TMH D.1328-1331, seen; (3) QVML 1978.5.76-78, (types 255-257) seen; (4) AMS I.20276-001-20278-001, seen; (2) BMNH 1978.6.1:2-3 seen; (5) FRD unregistered, seen; type locality: from amongst rocks around the shores of Lake Field, Julian Lakes, Tasmania).

DIAGNOSIS: Characterised by bullet-shaped form, dorsal fin high on back above pelvic fins, very short gill rakers, and two submandibular laterosensory pores. Differs from all other *Paragalaxias* in having the anterior interorbital pore well separated from the posterior nostril; from *P. dissimilis, P. eleotroides* and *P. mesotes* also in features listed in the diagnoses of these three species (pp. 570, 575, and 578 respectively).

DESCRIPTION: A small, stout species, the trunk rounded in section, somewhat flattened below but the back a little more arched; depressed anteriorly on head, compressed from above vent. Body deepest at about mid-way between pectoral and pelvic fins and tapering to the caudal peduncle which is long and slender, its length much greater than its depth. Head long, flattened below, snout long, bluntly pointed. Mouth large, only slightly oblique, reaching back to about anterior margin of eye, the jaws about equal in length, lips thick and fleshy. Eyes of moderate size, upper margins often projecting above upper head profile; interorbital broad, flat to slightly concave. Jaws without enlarged canine teeth laterally. Gill rakers very short, little more than stubs (Fig. 44). No pyloric caeca (Fig. 46).

Open pores on head small; disposition as shown in Fig. 47. Five pores in preopercular series; opening of anterior interorbital pore well separated from posterior nostril; two submandibular pores on each side.

Fins well developed. Dorsal fin inserted a little behind pelvic fin insertion and well behind mid-point of standard length; dorsal fin short-based and rounded, extending back well beyond fin base; anal fin much smaller, origin below or a little behind rear of dorsal fin. Pectoral fins small, fan-shaped, inserted low lateroventrally. Pelvic fins also small, inserted distinctly behind mid-point of standard length. Caudal fin slightly to moderately forked, fin tips rounded, fin depth somewhat less than greatest depth; peduncle flanges moderately developed.

Variation: meristic: see Table 19.
morphometric: see Table 20.

COLOUR: In life brownish to black-olive, markings varying from broken irregular patches to distinct and bold bars or reticulations, the background colour a yellowish-olive; belly a silvery-olive. Intensity and hue of colouration varies with colour of substrate. In preservative boldly contrasting dark grey and greyish-white.

SIZE: *P. julianus* is known to reach at least 99 mm L.C.F. (88.5 mm S.L.) and commonly exceeds 60 mm L.C.F.

NATURAL HISTORY: *P. julianus* was abundant amongst and beneath rocks on the beds of the lakes, particularly where the rocks were lying spaced apart on a gravelly substrate; less common amongst piles of rocks, where *Galaxias truttaceus* (Valenciennes) and *G. brevipinnis* Günther were much more abundant.

DISTRIBUTION: *P. julianus* is known from Lake Field, one of the uppermost lakes in the Julian Lakes system, from the main series of lakes in the system, which flow via the

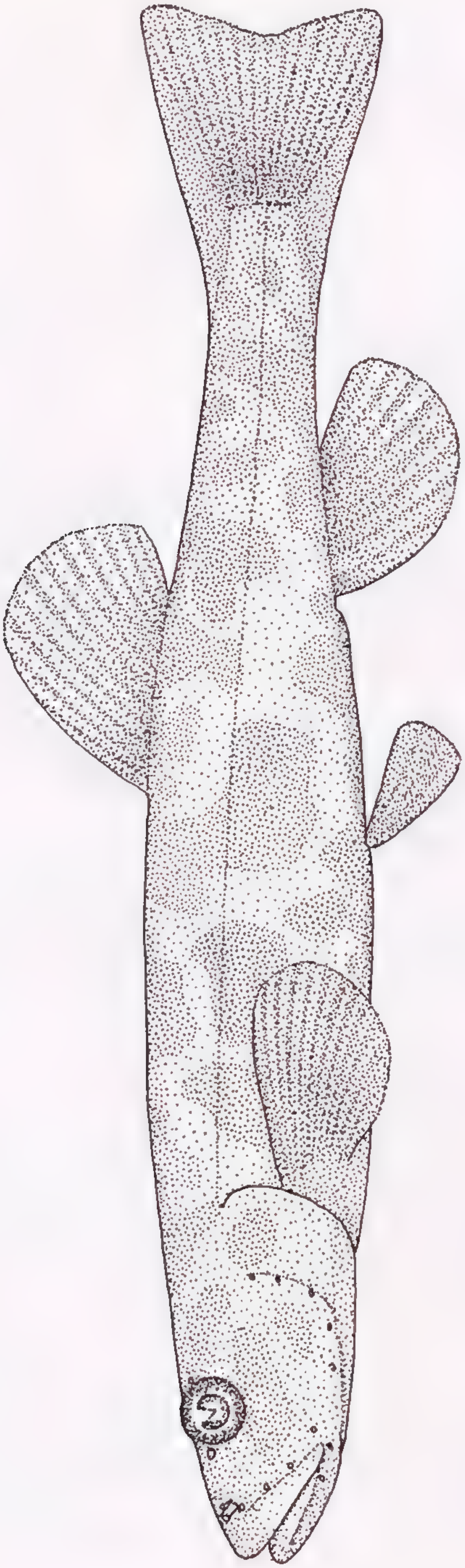

Fig. 42. *Paragalaxias julianus* McDowall and Fulton; Lake Field, Tas. 70.5 mm L.C.F.

Ouse River into Lake Augusta, from Carters Lake, from Lake Dudley which drains directly into Lake Augusta and from Ida and Talinah Lagoons and Lake Ada in the upper reaches of Little Pine River (Fig. 39). No attempt was made to sample Lake Augusta itself. This lake drains naturally via the Ouse River to ultimately join the Shannon River. (The Shannon RIver drains Great Lake, and finally joins the Derwent River). However, Lake Augusta water has been diverted, via the Liaweenee Canal, into Great Lake, where *P. dissimilis* and *P. eleotroides* are present. *P. julianus* does not yet seem to have made its way down the canal into Great Lake.

## SUMMARY

The family Galaxiidae includes 20 species in the Australian region, in three genera (*Galaxias* Cuvier, *Galaxiella* McDowall, and *Paragalaxias* Scott).

1. *Galaxias brevipinnis* Günther: (synonyms in general, recent usage include *G. coxii* Macleay, *G. weedoni* Johnston, *G. parkeri* Scott); known in coastal flowing rivers from central New South Wales (just north of Sydney), to eastern South Australia (near Adelaide), and widely in Tasmania; also present in New Zealand, Chatham, Auckland and Campbell Islands; a diadromous species with numerous landlocked populations, particularly in Tasmania.

2. *Galaxias olidus* Günther: (syn *G. schomburgkii* Peters, *G. ornatus* Castelnau, *G. bongbong* Macleay, *G. findlayi* Macleay, *G. kayi* Ramsay and Ogilby, *G. oconnori* Ogilby, *G. fuscus* Mack); known widely in moderate to high elevation rivers in the mountains of eastern New South Wales, Victoria and southeastern South Australia; confined to fresh water.

3. *Galaxias johnstoni* Scott: known only from Clarence Lagoon in the highlands of Tasmania; confined to fresh water.

4. *Galaxias pedderensis* Frankenberg: known from the Lake Pedder region, southwestern Tasmania; confined to fresh water.

5. *Galaxias fontanus* Fulton; newly described from the Swan River, eastern Tasmania; confined to fresh water.

6. *Galaxias truttaceus* Valenciennes: (syn. *G. occellatus* McCoy, *G. scopus* Scott, *G. truttaceus hesperius* Whitley); known from southern coasts of eastern and western Australia and widely in Tasmania; a diadromous species with landlocked populations in Tasmania.

7. *Galaxias auratus* Johnston: known from Lakes Sorell and Crescent in the highlands of Tasmania; confined to fresh water.

8. *Galaxias tanycephalus:* known only from Arthurs Lake in the highlands of Tasmania; confined to fresh water.

9. *Galaxias cleaveri* Scott: (syn. *Saxilaga anguilliformis* Scott, *G. upcheri* Scott); known from low elevation localities in northern, western and southeastern Tasmania; confined to fresh water.

10. *Galaxias parvus* Frankenberg: known from Lake Pedder and tributaries, and the upper Huon River, Tasmania; confined to fresh water.

11. *Galaxias maculatus* (Jenyns): (syn. *G. attenuatus* (Jenyns), *G. obtusus* Klunzinger, *G. parrishi* Stokell, *G. maculatus ignotus* Stokell); known in coastal flowing streams from southern Queensland to eastern South Australia, in southwards flowing

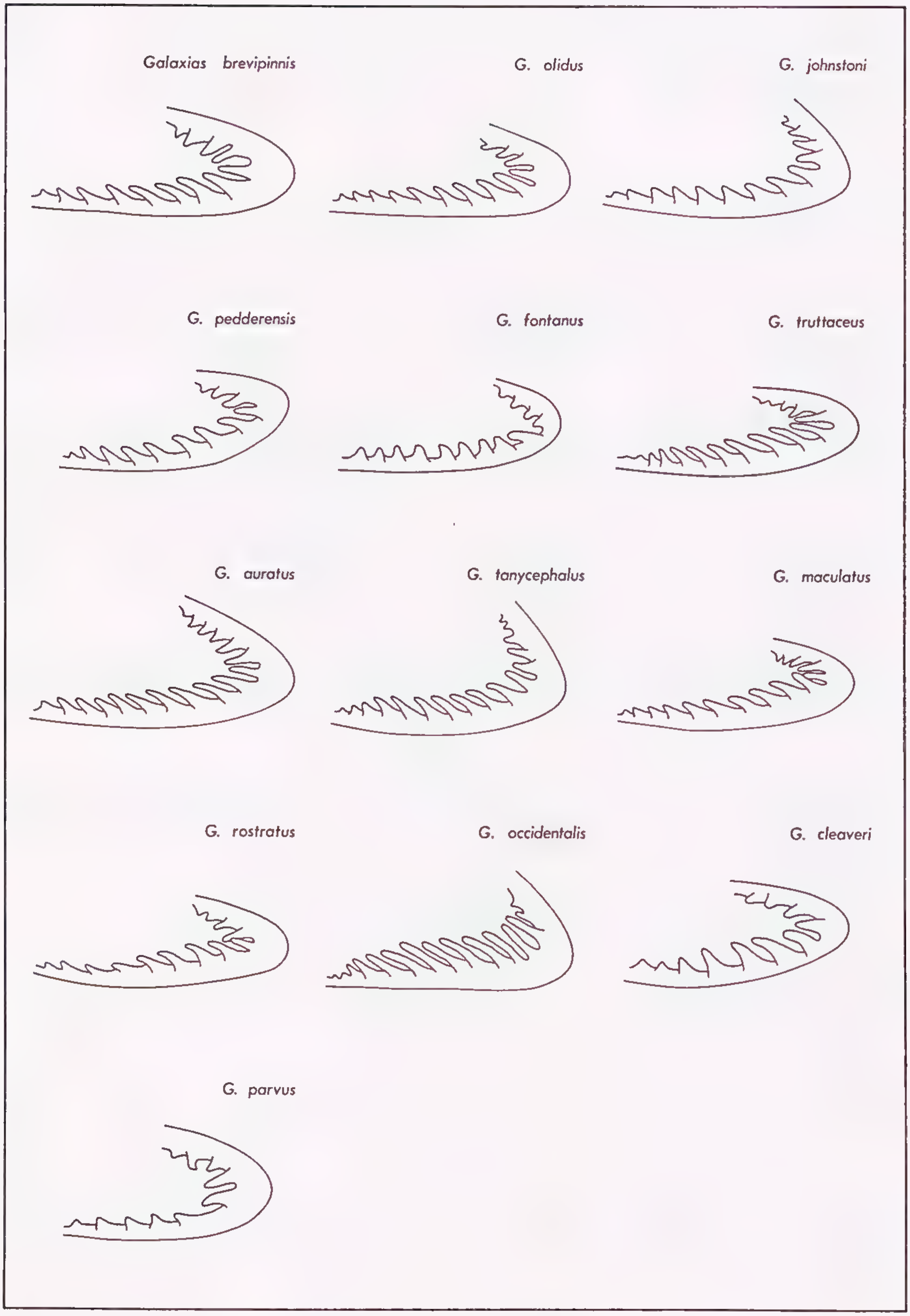

Fig. 43. Length of gill rakers in Australian *Galaxias* species.

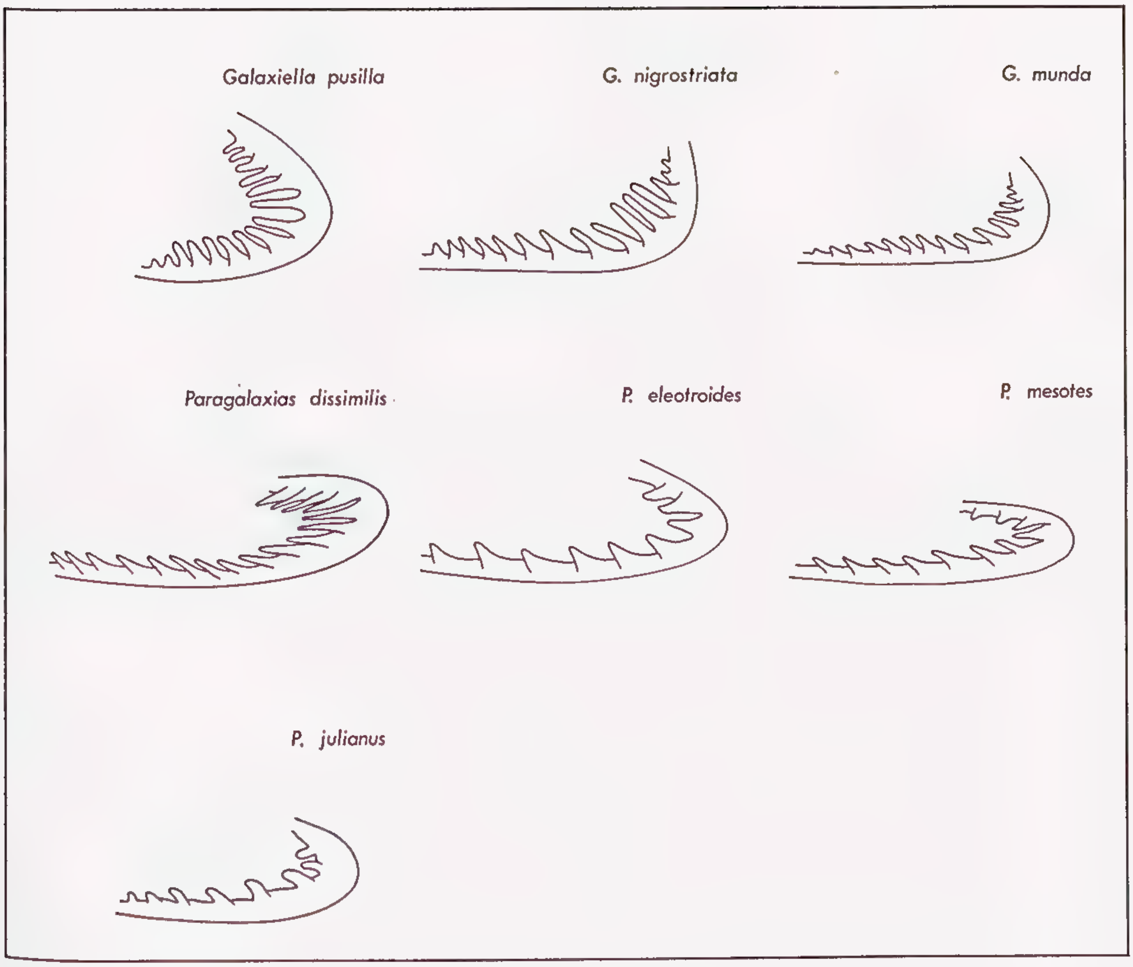

Fig. 44. Length of gill rakers in *Galaxiella* and *Paragalaxias*.

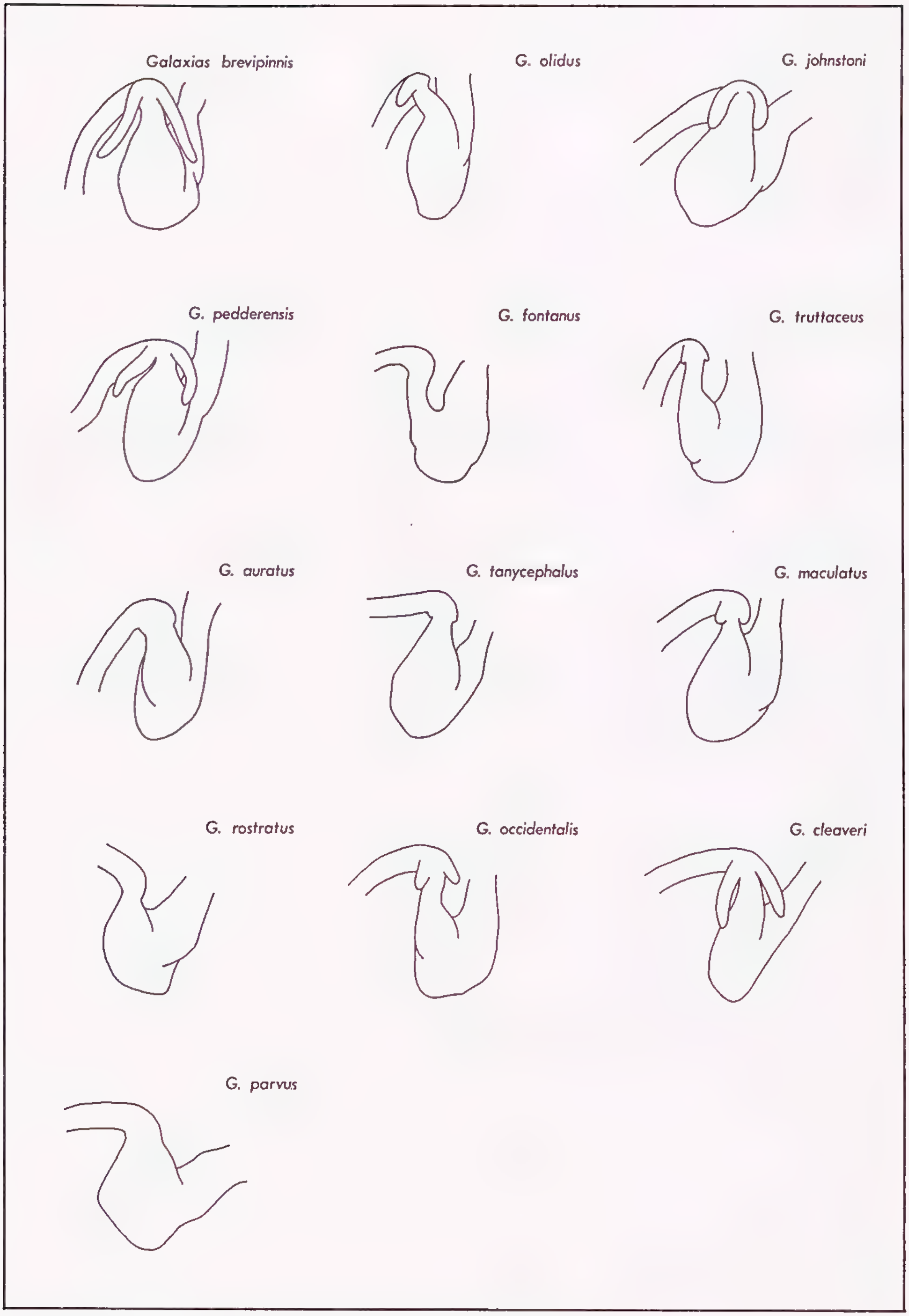

Fig. 45. Length of pyloric caeca in Australian *Galaxias* species.

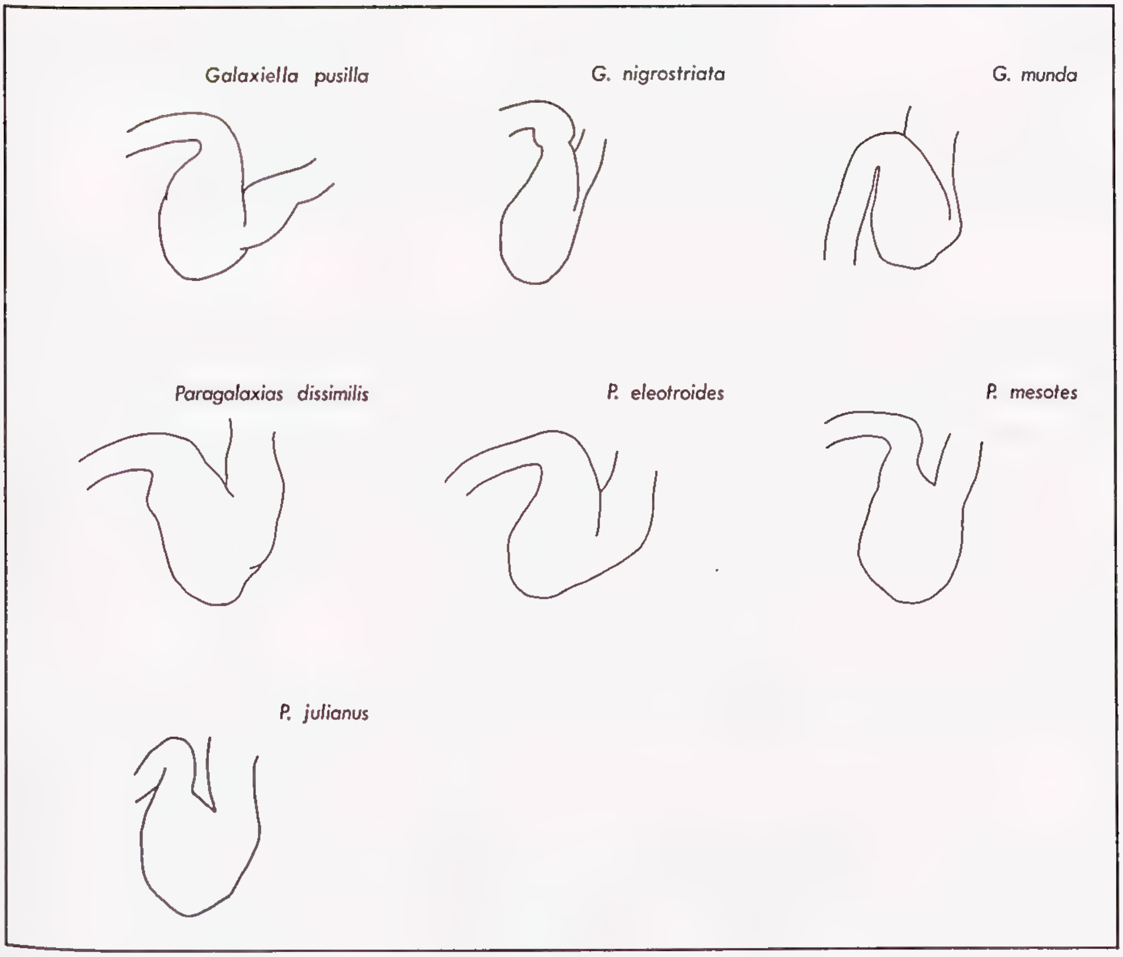

Fig. 46. Length of pyloric caeca in *Galaxiella* and *Paragalaxias*.

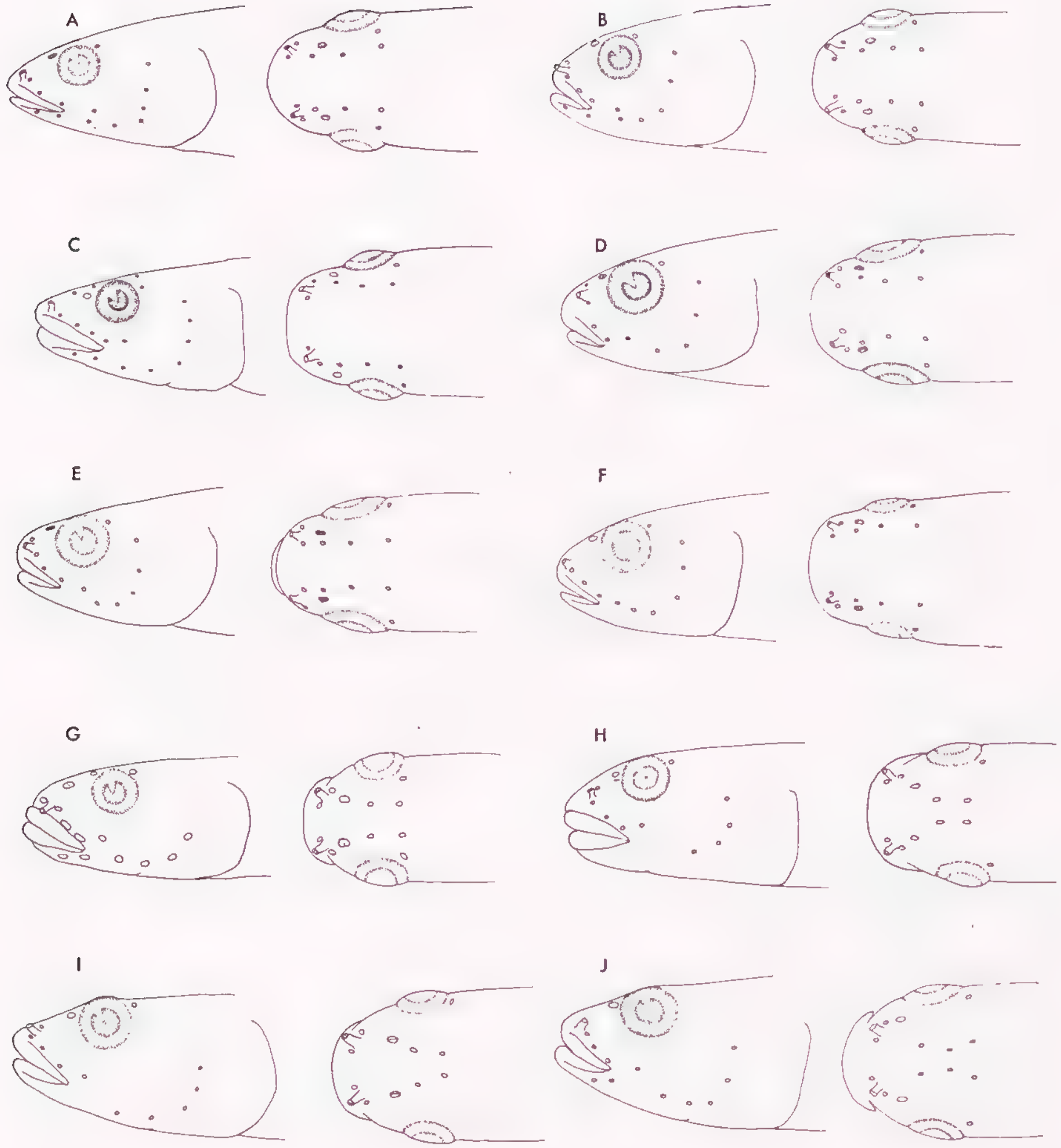

Fig. 47. Disposition of laterosensory pores in Australian galaxiid species. **a** most *Galaxias* spp (*Galaxias auratus* illustrated); **b.** *G. parvus;* **c.** *G. fontanus;* **d.** *Galaxiella pusilla;* **e.** *G. munda;* **f.** *G. nigrostriata;* **g.** *Paragalaxias dissimilis;* **h.** *P. eleotroides;* **i.** *P. mesotes;* **j.** *P. julianus.*

streams in Western Australia and widely in Tasmania; also occurs in Lord Howe Island, New Zealand, the Chathams, southern South America and the Falkland Islands; a diadromous species with numerous landlocked populations.

12. *Galaxias occidentalis* Ogilby: known in Western Australia from north of Perth, south and east towards Albany; confined to fresh water.

13. *Galaxias rostratus* Klunzinger: (syn. *G. planiceps* Macleay); known only in the Murray-Darling River system; confined to fresh water.

14. *Galaxiella pusilla* (Mack): (syn. *Brachygalaxias pusillus* (Mack), *B. pusillus pusillus* (Mack), *B. pusillus tasmaniensis* Scott, *B. pusillus flindersiensis* Scott); known in southeastern Australia from Gippsland west into eastern South Australia and in northern Tasmania; confined to fresh water.

15. *Galaxiella nigrostriata* (Shipway): (syn. *Brachygalaxias nigrostriatus* Shipway, known in Western Australia on the south coast between about Albany and Esperance; confined to fresh water.

16. *Galaxiella munda* McDowall: recently described from Western Australia where it is present in the far southwest (north of Perth to about Albany); confined to fresh water.

17. *Paragalaxias dissimilis* (Regan): (syn. *P. shannonensis* Scott); known from Great Lake, Shannon Lagoon and Penstock Lagoon in the highlands of Tasmania; confined to fresh water.

18. *Paragalaxias eleotroides* McDowall and Fulton: recently described from Great Lake and Shannon Lagoon in the highlands of Tasmania; confined to fresh water.

19. *Paragalaxias mesotes* McDowall and Fulton: recently described from Arthurs Lake and Woods Lake in the highlands of Tasmania; confined to fresh water.

20. *Pargalaxias julianus* McDowall and Fulton: newly described from the Julian Lakes and Lake Dudley in the highlands of Tasmania; confined to fresh water.

Although this revision is concerned primarily with the systematics of the Australian Galaxiidae, knowledge of the natural history of these fishes is briefly reviewed.

## ACKNOWLEDGEMENTS

The research upon which this revision is based results in part from work carried out at the Australian Museum (R. M. McD.) and in part from work done at the Department of Zoology, Melbourne University (R.S.F.).

The study of R.M. McD. was funded by a grant from the Australian Biological Resources Study. Thanks are due to the Interim Council of A.B.R.S. for their support, to the Trustees and Director of the Australian Museum for additional support, and to Dr. J. R. Paxton, Curator of Fishes at the Museum for much assistance during the work.

The study of R.S.F. was supervised by Dr M. J. Littlejohn and his assistance during the course of the study is gratefully acknowledged. The project was supported by Research Grants from the University of Melbourne.

The following assisted with the loan and/or gift of specimens: R. J. McKay, Queensland Museum; L. C. Llewellyn, New South Wales State Fisheries; I.S.R. Munro, Division of Fisheries and Oceanography, C.S.I.R.O.; J. M. Dixon, National Museum of Victoria; G. Apps, Fisheries and Wildlife Division, Victorian Ministry of Conservation; C. J. M. Glover, South Australian Museum; G. R. Allen, Western Australian Museum; R. H.

Green, Queen Victoria Museum; A. P. Andrews, Tasmania Museum; D. D. Lynch and W. Fulton, Tasmanian Inland Fisheries Commission; P. H. Greenwood and G. J. Howes, British Museum (Natural History); D. E. Rosen, American Museum of Natural History; G. von Wahlert, Staatl Museum für Naturkunde.

The following assisted in field work and collection and in various other ways: D. Blake, I. F. Briggs, D. Buckmaster, J. Frankenberg, S. Frankenberg, F. Hall, D. F. Hoese, P. Holbecke, A. Keast, J. Kusser, H. K. Larson, A. A. Martin, N. Morrisey, J. Parker, P. Parker, L. Pena, D. A. Pollard, P. A. Rawlinson, J. Renowden, P. Rogan, G. Stokell, A. H. Weatherly, W. D. Williams, C. S. Woods; to all of these go our thanks.

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## APPENDIX 1
## Material examined

Samples of galaxiid fishes listed below include samples from which morphometric and/or meristic data were taken, the data being presented in tables 1-20. The amount of data and the number of characters examined varies widely, from just a pelvic fin ray count to measurements and counts of all characters considered in the evaluation and distinguishing of species. When available, registration numbers for the samples are given, together with locality, repository of samples, and the number and length-range of specimens examined (all lengths, length to caudal fork in mm).

A detailed list of all material examined to ascertain distribution patterns of Australian galaxiids is available from the authors. A copy of this list has also been deposited in the Fish Department of the Australian Museum.

*Galaxias brevipinnis* Günther: New South Wales — Ourimbah Creek, (7 specimens 62.5-182 mm L.C.F.) AMS IB.747-8; Linden, Blue Mountains, (1, 163) AMS I.10429; Rivulet of Colo River, Mount Wilson, Blue Mountains, (12, 129.5-174) AMS I.8062-

8094; Gerringong Creek, Kangaroo Valley near Mossvale, (20, 111-152), AMS I.16930, AMS I.19035-001; South Australia — Tappanappa and Rocky River, Kangaroo Island, (7, 92-134) SAM F.2646, F.2672; Morialta Gorge, (5, 107.5-129) SAM F.1116; Yattalunga River, Cape Jervis, (1, 178) NMVM-; Victoria — Scrubby Creek cave 0.5 km from mouth, Buchan River (2) NMVM-; cave near Nowa Nowa, (1), NMVM-; Refuge Cove Creek, Wilsons Promontory, (2), FWDV-; Good Hope Creek, northeast Gippsland, (1) FWDV; Turtons Creek, (1) FWDV-; Lang Lang River, Heath Hill, (2) FWDV-; Henderson Creek, George River, (8, 79.5-152) NMVM-; Erskine River, Otway Range, (7, 113.5-170) NMVM 414-423; below Eucumbene Dam, Snowy River, (1, 200 mm) AMS I.17331; Lake Tarli Karng, Vic. (4) NMVM A.408-11; Tasmania — Samphire Creek about 1.5 km southeast of Strzelecki Peaks and Rhodes Creek, 11 km from Whitemark on road to Locotta, Flinders Island (7, 108.5-156.5) NMVM-; Dove River, Cradle Valley, (11) QVML-; Lake King William, (9) collection of E.O.G. Scott; Pine Creek, (17) TIFC-; Great Lake, (10, 63-106) FRD-.

*Galaxias olidus* Günther: Queensland — Condamine River, Warwick District, AMS IB.3777-8; Accommodation Creek, Severn River, Wallangara, (10, 62-83.5) AMS I.12440-8; New South Wales — Tenterfield, (10, 55.5-69.5) AMS I.17925; Anne River (10, 55.5-63) AMS I. 18913-001; Condobolin, Lachlan River (7, 49.5-95.4) AMS IB.2892; Lake Canobolas, Lachlan River, (10, 63-80.5) NSWSF-; Katoomba, (10, 47-62) AMS IB.3589, IB.5235; Towneys Creek, Anembo, Queanbeyan River (12), NMVM-; Burra Creek, Old London Bridge, Queanbeyan River, (15), NMVM-; creek 30 km from Brindabella Post Office on Rules Point Road, Goodradigbee River, (25) NMVM-; Happy Jacks Creek, Tumut River, N.S.W. (10, 70.5-87) AMS I.18874-001; Cockatoo Creek, 1.5 km north of Dundurrabin, Clarence River, N.S.W (4) NMVM-; Cordeaux Creek 3 km north of Berrima, Wollondilly River, (18) NMVM-; creek 5 km from Majors Creek on road to Tallaganda, Shoalhaven River, (7) NMVM-; Bells Creek 17.5 km south of Braidwood, Moruya River, (8) NMVM-; 1.5 km east of Delegate, Delegate River, (8) NMVM-; headwaters of Racecourse Creek, left branch above falls, Kiandra, Eucumbene River, (25) NMVM-; Australian Central Territory — Lake George, (11), NMVM-; Victoria — Cobungra River 1.5 km southeast of Mount Loch., Mitta Mitta River, (9) NMVM-; Middle Creek near Langfords Gap, Bogong High Plains, Mitta Mitta River, (11) NMVM-; tributaries of Pretty Valley Creek, Bogong High Plains, Kiewa River, (17) NMVM-; west branch of Kiewa River, (8) NMVM-; 1.5 km southwest of Tatra Inn, Mount Buffalo, Buckland River, (25) NMVM-; creek on Ovens Highway 27 km southeast of Wangaratta, Ovens River, (14) NMVM-; Scrubby Creek, near Alexandra, Goulburn River, (25) NMVM-; Strath Creek falls, 8 km southsouthwest of Strath Creek, Goulburn River, (25) NMVM-; tributary of McIvor Creek, 9.5 km from Tooboorac on road to Heatcote, Campaspe River, (13) NMVM-; Blackjack and Barker Creeks, Loddon River, (9) NMVM-; Smiggin Holes, Snowy River, (17) NMVM-; Mount Kosciusko, Snowy River, (25) NMVM-; Little Dargo River, Dargo High Plains, Mitchell River, (25) NMVM-; Shaws Creek, McAlister River, Benison High Plains, (13); Jerralong Creek, Latrobe River, Traralgon, (6) NMVM-; Clearwater Creek, Lerderderg Gorge, Werribee River, (12) NMVM-; Parker River above falls about 1.5 km from mouth, (7) NMVM-; Chapple and Charlies Creeks, near Lavers Hills, Gellibrand River, (15) NMVM-; Scotts Creek on Harraps Track, Glenelg River, Grampians, (9) NMVM-; Seymour Creek, Gellibrand River, Otways, (10, 78-107.5 mm) NMVM-; South Australia — First Creek, Waterfall Gully above falls, Torrens River, (25) SAM-; Myponga River above reservoir, (5) SAM; Fifth Creek, (6, 72-80 mm AMS I.5-7.

*Galaxias johnstoni* Scott: Tasmania — Clarence Lagoon, (2, 51-59.5) TMH D.1116, (3, 46-68) QVML 70, 71 (7, 50.5-86.5) AMS I.19593-001; (10, 48-98) FRD-.

*Galaxias pedderensis* Frankenberg: Tasmania — Stillwater Rivulet, Serpentine River, (5, 69.5-98) TMH D.1118; Swampy Creek, Upper Serpentine River, (4, 84-110.5) TMH D.1123; Hermit Creek, Hermit Valley, Upper Serpentine River, (10, 58.5-83.5) TMH D.1122; Serpentine River, (6, 57.5-102.5) TMH D.1121; Lake Pedder, near the mouth of the inflowing stream from Lake Maria (1) TMH D.941.

*Galaxias truttaceus* Valenciennes: Victoria — stream at Shelley Beach, (10, 85.5-168.5) AMS I.16985-003, I.16896-001; Growlers Creek on P.M.G. track to lighthouse, Wilsons Promontory, (9) NMVM-; Tasmania — Camp Creek, Currie Harbour, King Island (10, 87.5-145.0) NMVM-; Rhodes Creek, 11 km from Whitemark on road to Locotta (10, 86.5-119.5) NMVM-; Upper Scamandar and Wynyard, (25) NMVM-; Dover, Tas. (15) NMVM-; stream at Cox's Bight, (10, 91.0-145.0) NMVM-; Great Lake, (22, 67.0-133.5) FRD-; NMVM-; Western Australia — creek 4.5 km from Nanarup turn-off on road to Two Peoples Bay, Goodja River (7, 48.0-119.0), NMVM-; near Albany, (2, 64-67) AMS IB.280; Kalgan River above upper road bridge, (1, 119), AMS IB.1739; Creek flowing into Taylor Inlet, Nanarup (1) WAM P.2580.

*Galaxias auratus* Johnson: Tasmania — Lake Crescent, (20, 115.5-143.0) TMH D.1110.

*Galaxias tanycephalus* Fulton: Tasmania — Arthurs Lake, (20, 60-110.5) FRD-; TIFC-, AMS, I.19592-001, AMS I.19334-001, QVML 76/5/183, TMH D.1266, D.1267-9.

*Galaxias cleaveri* Scott: Tasmania — Punchbowl Creek, Tamar River, (3, 46.5-60.5) QVML 1975.5.558; Pieman River, (3, 60.5-80.0) QVML 1975.5.77; Queenstown, (8, 69.0-102.0) AMS IA.3488; Melaleuca, Port Davey, (6, 90.5-119.5) TMH D.1150; Esperance River, Dover, (1, 65) CSIRO B.229, (5, 63.0-101.5) TMH D.1149, (2, 47.0-73.5) TMH D.1148.

*Galaxias parvus* Frankenberg: Tasmania — Anabranch of Huon River 5 km south-southeast of HEC Hut, (12, 42.0-55.5) NMVM-; River below Trappes Hill, Lake Pedder, (9, 59.0-78.5) TMH

*Galaxias maculatus* (Jenyns): Diadromous Populations: New South Wales — St. Albans Common, Hawkesbury River, (9, 63.5-142.0) AMS I.18857-001; Gulpa Creek, Tuross River, (10, 95.5-150.0) AMS I.15857-001; Victoria — drain about 5 km along Denham Road from Rossiter Road, Kooweerup, (10, 82.0-119.0) NMVM-; streams on Wilson's Promontory, (10) NMVM-; Toomuc and Cardinia Creeks, (25) NMVM-; Browns Creek, 400 m upstream, Otway Range, (10, 63.5-122.0) FWD-; South Australia, — Port Lincoln, (10), SAM F.96; Port Macleay Jetty, (18) SAM F. 1102; Breakneck River, Flinders Chase, Kangaroo Island, (25) NMVM-; Tasmania — streams on Flinders Island (10) NMVM-; creeks northwest of Gladstone, (10, 72.5-98.0) AMS I.17579-002; Nelson River, (10, 83.5-100) AMS I.17587-002; Derwent River, Hobart, (1, 92), FRD-; Orielton Lagoon, (9, 71.0-114.5) FRD-; Huon River, (7, 78.5-113.0) FRD-; Lacustrine populations: New South Wales — Lake Windimere, Jervis Bay, (10, 60.0-89.0) AMS I.17444-002; Victoria — Lake Corangamite, (10, 67.5-102.0) AMS I.16989-009; Lake Modewarre, (10, 86.0-130.0) FRD-; Lake Bullen Merri, (10, 68.0-101.0) FRD-; Lake Colac, (10, 65.0-84.5) FRD-; Lake Purrumbete, (25) NMVM-; Wurdiboluc Reservior, (6) NMVM-; Lake Bongbong, (20) NMVM-; near Lake Wangery, (10) NMVM-; Western Australia — Pallinup River south of Formby, (12) WAM P.8042; Gairdner Lake, (10, 73.5-97.5) AMNH 33612; Fitzgerald River, (10, 68.5-125.5) AMNH 36616; Hammersly River 53 km from Ravensthorpe on road to Ongerup (25) NMVM-; Dalyup River 36.5 km from Esperance on road to Ravensthorpe, (15, 48.5-77.5) NMVM-; Shark Lake, near Esperance, (8) WAM P.8043-50; Dandy Creek, (17) NMVM.

*Galaxias rostratus* Macleay: New South Wales — Rankins Lagoon at Bathurst, (4, 104.0-116.0) MS I.16261-001; Victoria — Colbinabbin, (15, 83.0-110.0) NMVM —; Third Reedy Lake, near Kerang, (7) NMVM —.

*Galaxias occidentalis* Ogilby: Western Australia — Twin Swamps Reserve, Bickley, about 40 km northnortheast of Perth, (7) NMVM —; pool in upper Swan River 1.5 km north of Walanga, (10, 60.0-76.0) AMNH 31474; Blackwood River, 100 m down from Sues Road Bridge, (10, 69.0-109.5) AMNH 31477; pool 13.5 km south of Northcliffe on Windy Harbour Road, (10, 65.5-115.0) AMNH 31476; Shannon River at Shannon River Mill, (5) NMVM —; Waychinnicup Creek 11 km west of Cheyne Beach, (7) NMVM —; pool under bridge near Elleker turnoff at Marbellup (1) NMVM —.

*Paragalaxias dissimilis* (Regan): Tasmania — Great Lake, (20, 43.5-63.0), FRD —.

*Paragalaxias eleotroides* McDowall and Fulton: Tasmania — Great Lake, (20, 37.0-51.5) FRD —; AMS I.19152-001; QVML 1976.5.166; TMH D.1259, D.1261-2; BMHN 1976. 8.13:6-7.

*Paragalaxias mesotes* McDowall and Fulton: Tasmania — Arthurs Lake, (20, 41.0-69.0) FRD —; AMS I.19151-001; TMH D.1260, D.1263-5; QVML 1976.5.167; BMNH 1976.8.13:4-5.

*Paragalaxias julianus* McDowall and Fulton: Tasmania — Lake Field, (6, 41-62.5) TMH D.1327, TMH D.1328, AMS I.20276-001, QVML 1978/5/76, BMNH 1978.6.1:3, Julian Lakes, (6, 51-83.5), TMH D.1329-30, AMS I.20277-001, QVML 1978/5/77, BMNH 1978.6.1:2, FRD —, Lake Dudley, (18, 43.5-74), TMH D.1331, AMS I.20278-001, QVML 1978/5/77, FRD —.

*Galaxiella pusilla* (Mack): Victoria — drain flowing into Narracan Creek, La Trobe River system, (20, 24.0-34.0) FRD —; (7, 24.75-33.75), Cardinia Creek, (1, 25.75, 2 unmeasured), AMS IB 1999/3199; Eumeralla R, 5 km west of Yambuk, (1, 24.25) NMVM —; Tasmania — AMS I.17251; Blackman's Lagoon, (4, 24-25.75) FRD —.

*Galaxiella nigrostriata* (Shipway): Western Australia — small swamp 100 m E of Gledhow South Road on road to Elleker (1, 29.5) NMVM —; drain 100 m north of Elleker-Albany Road on Marbellup Road, (5, 24.5-34.75) NMVM —; Marbellup Creek, Elleker, (2, 26.5, 21.5) AMS IB.3197-8; drain entering Marbellup Creek at Elleker, 16 km west of Albany, (8, 24.5-28.75) NMVM —.

*Galaxiella munda* McDowall: Western Australia — pool in jarrah forest about 8 km north of Scott River, south of Canebreak Yards, between Nanup and Augusta, (10, 29.25-39.0), WAM P.25736-001, WAM P.5225, AMS I.19522-001; creek 10 km eastnortheast of Shannon River (type locality of *Lepidogalaxias salamandroides* Mees), (9, 28.5-41.0) WAM P.8067; creek 4.6 km from Nanarup turnoff on road to Two People's Bay (4, 25-36), NMVM —; Carey Brook, Donnelly River, a small, clear jungle stream, near Jasper Road and Boat Landing, south of Nanup, 37 km west of Pemberton, (2, 35.5), WAM P. —; creeks and waterholes at Walpole, (2, 36.5, 38.0) WAM P. —.

Manuscript accepted for publication 12 July, 1979.

# FIRST COMPLETE SPECIMEN OF THE DIPNOAN *GOSFORDIA TRUNCATA* WOODWARD FROM THE TRIASSIC OF NEW SOUTH WALES.

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NATIONAL MUSEUM
15 OCT 1981
OF VICTORIA

## SUMMARY

*Gosfordia truncata* Woodward is based on several incomplete specimens found in the 1880's. The recent discovery of the first complete specimen of *G. truncata* in a Triassic shale lens near Gosford, New South Wales, makes possible the first restoration of the species and clarifies its relationships with other dipnoans, living and extinct.

## INTRODUCTION

Of all the continents, Australia has the longest documented record of lungfish (or dipnoan) evolution (Hills 1958, 103) ranging from the early Devonian marine genus *Dipnorhynchus* (Thomson and Campbell 1971) to the extant Queensland freshwater form, *Neoceratodus forsteri* (Krefft 1870). Until the recent discovery of well-preserved, articulated dipnoan remains in the marine late Devonian Gogo Formation of the Kimberleys, Western Australia (Miles 1979) and in the late Devonian continental deposits of the Mt. Howitt Province, central Victoria (Marsden 1976, 122) few Australian fossil dipnoans have been represented by material sufficiently well-preserved to allow complete restorations to be made.

This certainly applied to *Gosfordia*, a poorly known, early Triassic dipnoan recovered in the 1880's from a shale horizon near the top of the Gosford Formation in the Narrabeen Group of the Sydney Basin (cf. Packham *et al.*, 1969, 407). The original material of *Gosfordia* (and of several other species of Triassic fishes) was uncovered near the town of Gosford, 50 km north of Sydney, N.S.W. during the excavation of a quarry for railway ballast materials. The Railway Ballast Quarry yielded over 400 fossil fish specimens and a labyrinthodont amphibian. Included amongst the fish specimens, which were predominantly actinopterygians, were five incomplete specimens which Woodward (1890, 4-6, Pl.1 figs 1, 2, Pl. II figs. 1, 2) attributed to a new genus and species of dipnoan which he named *Gosfordia truncata*.

Ninety years after the discovery of *Gosfordia*, and almost exactly 110 years after William Forster, a Queensland squatter, sent to Gerard Krefft in Sydney the first specimens of the living lungfish which now bears his name, *Neoceratodus forsteri* (Krefft), The Australian Museum unexpectedly acquired another remarkable lungfish specimen — the first complete example of the Triassic dipnoan *Gosfordia* (AM F.60621).

The new specimen of *Gosfordia* (Fig. 1) was discovered by an observant quarryman, Mr John Costigan, employed by Glendale Wash Sands Pty. Ltd. which operates a quarry in the Somersby Falls area, west north west of Gosford and only 6-7 km away from the type locality. Mr Costigan noticed a small part of a largish fish exposed on a block of shale and split it to reveal a complete and remarkably well-preserved specimen of unusual type. Shortly afterwards the fish fossil was acquired by an amateur collector, Mr Colin Chidley of Sydney who recognised its unique scientific importance and passed it, in turn, to The Australian Museum for safe-keeping and scientific study.

The quarry from which the *Gosfordia* specimen came works an extensive shale lens in the Hawkesbury Sandstone. The massive, grey silty shale, up to 3.4 m thick, is used for brickmaking materials whilst the considerable thickness of overlying, weathered yellow

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sandstone is stripped off and processed for building sands. Fish fossils have turned up on several occasions during the quarrying of the shale but, because of the extraction methods, it has not yet proved possible to locate the level (or levels) from which the fish come.

Recent investigations by the N.S.W. Geological Survey (Uren 1974) have shown that this particular shale lens lies within the Hawkesbury Sandstone, at least 60-70 m above its base. It is thus stratigraphically higher and geologically later than the original fish-bed in the Railway Ballast Quarry which lies near the top of the underlying Narrabeen Group. Shale lenses in the Hawkesbury Sandstone throughout the Gosford area cover areas of up to 8 hectares and vary in thickness from 2-6 m. They appear to represent temporary lakes or cut-off loops of large river systems in Triassic times.

## DESCRIPTION OF THE SPECIMEN

The entire fish is clearly visible on the larger of the slabs of grey shale and most of the counterpart (with the exception of much of the head) was recovered on various large flakes which have since been reassembled into a smaller block. Like all the other fish fossils from the Gosford area this latest specimen is largely reduced to a carbon film with very little surface relief. By good fortune the specimen of *Gosfordia,* which measures 50 cm from nose to tail, lies neatly just within the margins of the enclosing block, having been narrowly missed both by the bulldozer blade and by the quarryman's chisel!

The fish is seen entirely in lateral view, confirming Woodward's interpretation (1890,5) that the animal was laterally compressed in life. The median fins are beautifully preserved with a minimum of disturbance and with even the finest of fin-rays visible. The paired fins are also visible, projecting clear of the ventral margin of the trunk.

### HEAD REGION

As observed by Woodward (1890,5) the head of *Gosfordia* is subtriangular and very small relative to the size of the animal, measuring only 6 cm from the posterior margin of the opercular plate to the snout. Because of the crushed, heavily carbonised nature of preservation the fine details of the bones in the head region are difficult to identify and trace and the new specimen, unfortunately, adds little to that figure by Woodward (1890, Pl.I fig. 1; AM F.50975). The outline of the cleithrum is reasonably clear (Figs. 1, 2B) as a longish, narrow, curved plate. With less certainty one can determine the position of the orbit and the outline of a subcircular operculum bordered ventrally by narrow subopercular plates (Fig. 2B). In the skull roof, normally one of the most useful regions for dipnoan comparative anatomy, very little can be determined with accuracy.

The only possible evidence of the crushing toothplates consists of several indistinct ridges disappearing under the head. If correctly identified as a toothplate these must have been much more weakly developed in *Gosfordia* than in its contemporary, *Ceratodus,* or in the extant *Neoceratodus.*

### TRUNK

The new specimen of *Gosfordia* reveals the fish to have been remarkably deep-bodied for a lungfish and, presumably, laterally compressed. Most of the area of the fossil is covered by an evenly carbonised film which probably represents the original squamation. Woodward (1890,6) noted that the scales were "evidently very small, and all are marked by fine longitudinal striations" but was unable to distinguish their precise outlines. It seems probable that the squamation extended distally over much of the lateral surface of the median fins as depicted by Goodrich in *Neoceratodus* (1904, Pl.35, fig. 3) and by Jarvik (1959 figs. 17A, B) in both *Scaumenacia* (late Devonian) and

*Neoceratodus* (Recent), forms separated by about 350 million years. The new *Gosfordia* (Fig. 1) displays a marked, narrow zone of disturbance and minor crumpling extending right around the median fin between the outer margin and the axial skeleton. This line may mark the transition between the more fleshy proximal region and the thinner distal part of the fin.

The presence of a long narrow, clear strip running the length of the trunk indicates that the notochord was persistent and unconstricted and that none of the associated vertebral structures were ossified. Distally it tapers to a sharp point at the termination of the caudal fin.

The ribs are moderately well-preserved. They were long, slender and gently arched and, in several places, both left and right ribs are visible and superimposed. Allowing for this there appear to be about 25-27 pairs of ribs in *Gosfordia* (Fig. 2B) compared with some 26 pairs in *Neoceratodus* (Fig. 2A).

The neural and haemal arches and rods were lightly ossified and, although their general arrangement is quite clear, some details are difficult to determine accurately. In *Gosfordia* (Fig. 2B) as in *Neoceratodus* (Fig. 2A) there appear to be three series of ossified rods in the dorsal axial skeleton and in the ventral region posterior to the rib-cage. In *Gosfordia* the middle row is extremely faint and has thus been more tentatively restored.

The greatest depth of the trunk (not including the fins) is about 15 cm but a marked bulge along the ventral margin probably indicates that the soft, unsupported underbelly collapsed in the mud during burial. In restoring *Gosfordia* (Fig. 2B) the writer has allowed for the original roundness of the trunk and has reduced the overall depth to 14 cm.

## MEDIAN FINS

In *Gosfordia,* as in virtually all post-Devonian dipnoans (Fig. 3) the caudal, dorsal and anal fins have so completely fused as to leave little evidence of their former extent. The caudal fin of *Gosfordia* (Figs. 1, 2B; Woodward 1890 Pl.I, fig. 2) is diphycercal and very large, even by dipnoan standards. It extends along the dorsal margin for 30 cm (60% of the total length) and along the ventral margin for 20 cm. It is also very deep, reaching about 16.5 cm between the highest point on the epichordal (dorsal) lobe which lies slightly anterior to the lowest point on the hypochordal (ventral) lobe. Posteriorly the caudal fin terminates in a blunt point which subtends an obtuse angle of about 115° in contrast to all other dipnoans (Fig. 3) where the termination of the caudal fin is acute-angled.

## PAIRED FINS

One example of each of the pectoral and pelvic fins is preserved and clearly visible outside the remains of the trunk. The proximal portion of the pectoral fin was later excavated in the counterpart and, although not particularly well-preserved, appeared to indicate that the fin was inserted about halfway along the posterior cleithral margin. The pectoral fin is extremely long (15-16 cm), narrow (1.8 cm) and lanceolate, tapering to a fine point. The fin-rays are equally well-developed along the anterior and posterior margins of the fin but no trace remains of the axial elements of the fin endoskeleton. In shape and structure the pectoral fin of *Gosfordia* more closely resembles the very specialised pectoral fin of *Protopterus* (Fig. 3) than the shorter, more powerfully built fin of *Neoceratodus* (Fig. 2A). It is now clear that the specimen tentatively identified by Woodward (1890 Pl.II fig. 2) as a pectoral fin of *Gosfordia* does not belong to this genus; it is more likely to belong to the long-bodied actinopterygian, *Saurichthys,* which is also present in the same horizon.

The pelvic fin of *Gosfordia* is similar in shape to the pectoral but much shorter (about

8 cm) and presumably less mobile in life. There is no visible evidence in the *Gosfordia* material of a pelvic girdle similar to that still present in *Neoceratodus* (Fig. 2A).

The pectoral and pelvic fins of *Gosfordia* were clearly rather feeble structures which, like those of *Neoceratodus,* were used in sculling during slow locomotion and probably also for "walking" along the bottom or in resting on the bottom with the head raised up. This would only apply of course, when the fish was totally submerged and the weight supported by the water. It is also possible that the *Gosfordia* pectoral fins acted as sensory feelers (similar to those of *Protopterus* and *Lepidosiren)* which would have been of considerable use in very murky waters as suggested by Thomson (1969a, 118); the lithology of the Hawkesbuy shale lens indicates rather muddy bottom conditions at the time of deposition.

## ASSOCIATED FAUNA

In 1972 quarrying operations in the same general area, and working the same shale lens, as the latest find brought to light numerous, well-preserved specimens of fossil fish. A joint party from The Australian Museum and the N.S.W. Mines Department collected several specimens most of which appear to belong to *Zeuchthiscus australis* (Woodward). This species was based initially (1890, 3l, p1.IV, fig. 2; *Semionotus australis* Woodward) on a single imperfect specimen from the Railway Ballast Quarry. Wade subsequently recognised other specimens in the same collection and redescribed and renamed the species as *Zeuchthiscus australis* (Wade 1939, 214-6, Pl.IX, fig. 4). The only significant difference between 1890 and 1972 finds (which are now housed in The Australian Museum; AM F.55094-55107), is in their relative sizes. The specimens from the Railway Ballast Quarry apparently reached a length of about 16.5 cm whilst the 1972 finds from the new quarry included several specimens around 25 cm in length.

The only other fossil fish recorded from this horizon, to date, is a very fine specimen of *Saurichthys gigas* (Woodward) which was discovered in 1972 by the same Mr J. Costigan who found the latest *Gosfordia.* This *Saurichthys* (AM F.55091-2), as preserved, extends from the tip of the snout to just posterior to the pelvic fins and is 70 cm. long. Using the earlier Railway Ballast Quarry specimens of *Saurichthys* as a guide (Woodward 1890, Pl.IX, figs. 1,2; *Belonorhynchus gigas* Woodward) it is possible to estimate that the original total length of the specimen from the new quarry must have been half as long again, around 105 cm from nose to tail. Woodward's material indicated a length of around 49 cm for *S. gigas* but he mentioned (1890,23) that it probably attained "sometimes much more".

## *GOSFORDIA* AND THE EVOLUTION OF DIPNOI

Dipnoan evolution has long been a subject of interest and debate, and there remain conflicting opinions as to the relationships of dipnoans and other groups of bony fishes which appeared about the same time in the early Devonian. Fortunately the dipnoans have left us a fairly good fossil record and three living genera which allow us to study their soft parts and living habits. A representative selection of dipnoan genera for which there are good body fossils available is presented (Fig. 3) for comparison with *Gosfordia.* Many other genera and species are represented only by isolated toothplates, or by skulls or cranial roofs. There are also conflicting views on the possible interrelationships of the various lines of dipnoan evolution which have been identified (e.g. Bertmar, 1968; and Thomson and Campbell 1971, 102, fig. 35, who have attempted to depict the phyletic relations of known Palaeozoic Dipnoi).

The examples used here (Fig. 3) are arranged both stratigraphically and (from left to right) to illustrate the range in body forms from more "conservative" to more "progressive" genera. As Westoll (1949) and others have demonstrated the Dipnoi evolved rapidly during the Devonian and by Permo-Carboniferous times had achieved a basically "modern" body form.

The earliest well-known genera, *Uranolophus* (Denison 1967) and *Dipnorhynchus* (Thomson and Campbell 1971) from the early Devonian, were marine fish as were many other Devonian dipnoan genera but the majority of later forms have been freshwater inhabitants (Thomson 1969b, table 1, 461). *Dipterus* and *Pentlandia* (Fig. 3) from the Middle Devonian do not differ greatly in their external morphology from contemporary crossopterygians (e.g. *Osteolepis*) in which the two dorsal fins and the single anal fin were separate and the caudal fin was normally heterocercal. By late Devonian times several lines of dipnoan evolution had produced a wide range of body forms ranging from the "conservative" *Rhynchodipterus* (Fig.3) through *Fleurantia* and *Scaumenacia* (with enlarged posterior and reduced anterior dorsal fins) to more "progressive" forms such as *Phaneropleuron*. In the last genus the dorsal fins had merged with the caudal and only the anal fin remained separate.

By Carboniferous and Permian times even this fin had been incorporated in the caudal fin complex as in *Uronemus* and *Conchopoma*. Major changes were still taking place in the skull, dentition, axial skeleton etc. but the body form was essentially modern.

Although *Gosfordia* is usually placed in the family Ceratodontidae (Thomson 1969a, 93) it is now clear that it must be considered an aberrant offshoot from the main line of ceratodontid evolution. The genus *Ceratodus* was already in existence by early Triassic times and a contemporary of *Gosfordia*. *Ceratodus*, which survived into late Cretaceous times, has been recorded from North America, Europe, Asia, Africa and Australia (Schaeffer 1969) although most of the occurrences, unfortunately, consist only of isolated toothplates and complete body fossils of the genus are rare.

Two occurrences of *Ceratodus* have been recorded from the Triassic rocks of the Sydney Basin. A small lungfish specimen, only 9.5 cm long, was described by Wade (1935, 1-3, Pl.I) from the Middle Triassic fish-bearing shale lens in the Hawkesbury Sandstone formerly quarried on Beacon Hill, Brookvale, a Sydney suburb. The unique holotype of *Ceratodus formosus* Wade (B.M.N.H. P16828) may well be a juvenile (Wade records the findings of several large, isolated dipnoan scales in the Brookvale horizon) but the relative proportions of the head, trunk and fins rule out any possibility of a close relationship to *Gosfordia*.

The other Sydney *Ceratodus* record came from the Middle Triassic shale horizons in the later Wianamatta Group, from now disused quarries in the suburb or St. Peter's. *Sagenodus laticeps* Woodward (1908, 6-8, Pl II, figs. 1, 1a) was later reassigned to *Ceratodus* by Wade (1931, 123) in his review of Australian Mesozoic fishes. *Ceratodus laticeps* (Woodward) is represented by a single incomplete specimen consisting of the central region of the trunk of a rather large, deep-bodied dipnoan. The head region is not well preserved but clearly displays a fused pair of fairly massive palatal toothplates which indicate that the proportions of the head must have been considerably more substantial than the head of a *Gosfordia* individual of comparable body size.

Whether or not these two occurrences have been correctly assigned to *Ceratodus* remains uncertain. There is no doubt, however, of the validity of Woodward's genus *Gosfordia*, a distinctive, deep-bodied dipnoan of early-Middle Triassic times. In many respects *Gosfordia* is more specialised than either *Ceratodus* or its descendant *Neoceratodus*, which has remained essentially unchanged at least since Cretaceous times and probably much longer.

From our knowledge of the mode of life of the three living lungfish genera it would appear that *Gosfordia* had most in common with *Neoceratodus*. Both *Protopterus* and *Lepidosiren* possess the ability to burrow and aestivate (or hibernate), a dipnoan survival device which is known to have been employed by some members of the group as early as Permo-Carboniferous times (e.g. *Gnathorhiza*). Although some workers (e.g. Thomson 1969, 128-9) have noted physiological evidence which might indicate that the ceratodontid (as well as the lepidosirenid) dipnoans may once have been able to aestivate, the extant *Neoceratodus* does not possess this ability. From its shape it seems quite unlikely that *Gosfordia* could either burrow or aestivate; on the contrary it gives the impression of having been a rather active, powerfully built swimmer and the size of the caudal fin suggests it could move quite fast when necessary.

## ACKNOWLEDGEMENTS

The discovery of a complete *Gosfordia* illustrates dramatically the major contributions to science which may be made by excavation workers in quarries, mines, roadworks etc. who are in an unrivalled position to observe and save unique geological specimens for scientific study and for public display in State museums. All too often such specimens are ignored and needlessly destroyed. The writer wishes to acknowledge the contributions of Mr John Costigan (discoverer of the new *Gosfordia*), Mr C. Chidley, Sydney (who passed it to The Australian Museum), Mr R. Munday, Manager, Glendale Wash Sands Pty. Ltd., Mr John Fields, The Australian Museum photographer (for Fig. 1).

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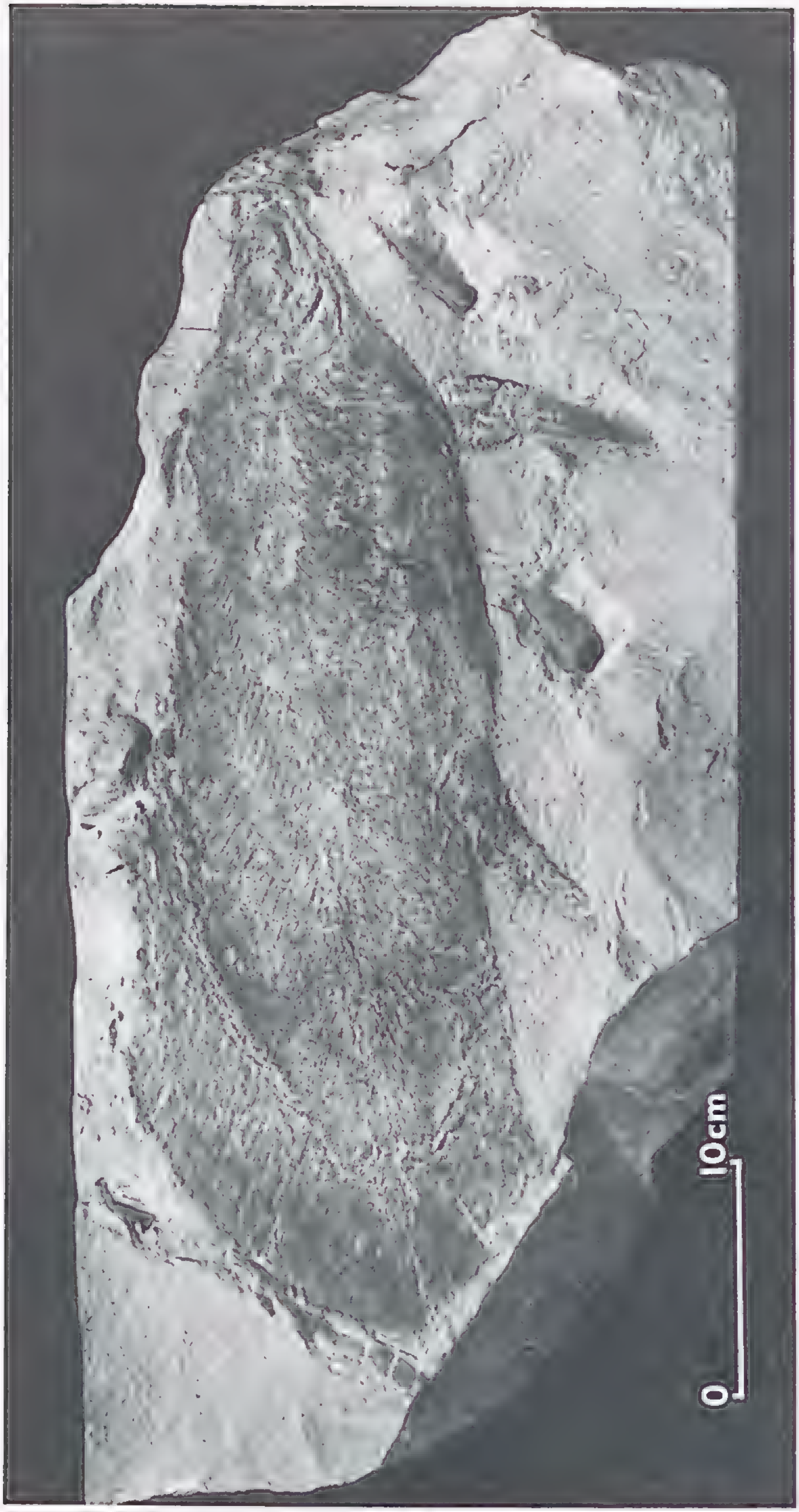

Fig. 1. *Gosfordia truncata* Woodward. Triassic, from shale lens in Hawkesbury Sandstone, 7 km. WNW of Gosford, New South Wales. Scale equals 10 cm. Australian Museum F.60621.

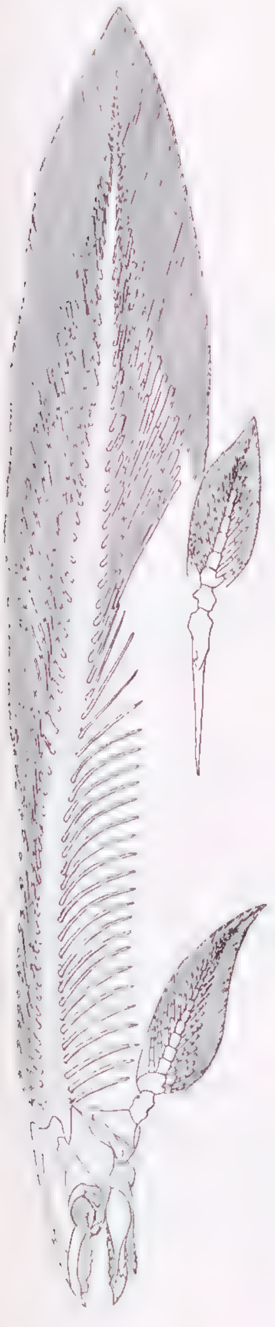

Fig. 2A. *Neoceratodus forsteri* (Krefft). Recent, Queensland. Modified after Günther, 1871 (post-cranial skeleton) and Goodrich, 1930 (cranial skeleton).

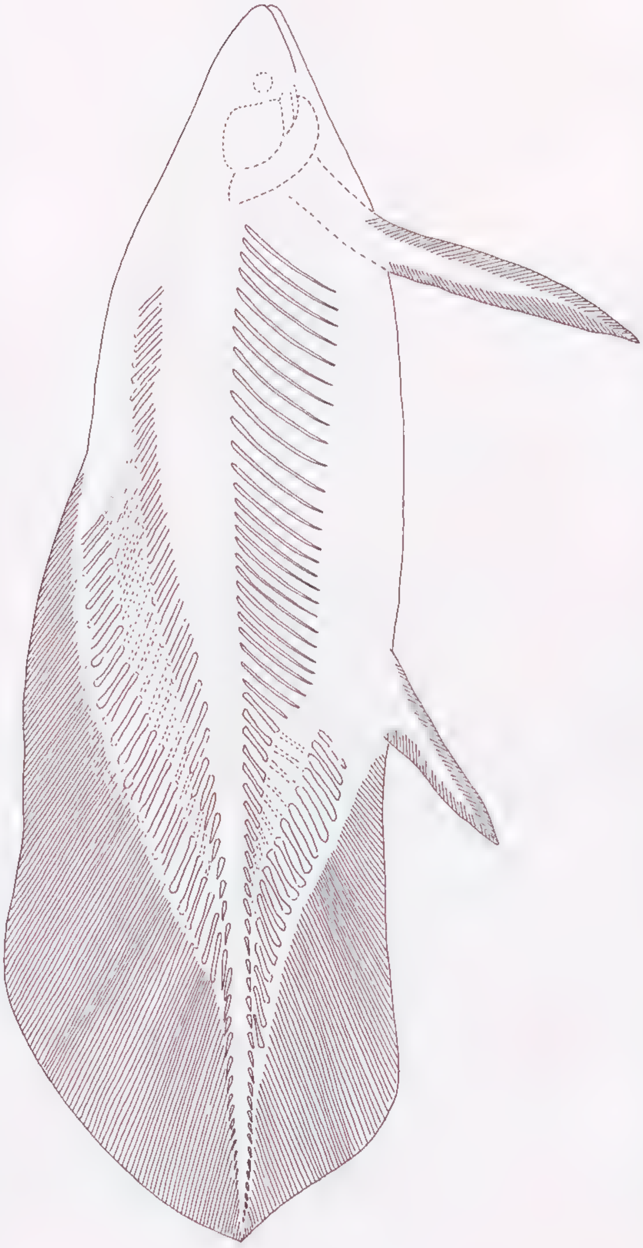

Fig. 2B. *Gosfordia truncata* Woodward. Triassic, New South Wales. Skeletal restoration based on A.M. F.60621 (Fig. 1). Length of original specimen 50 cm.

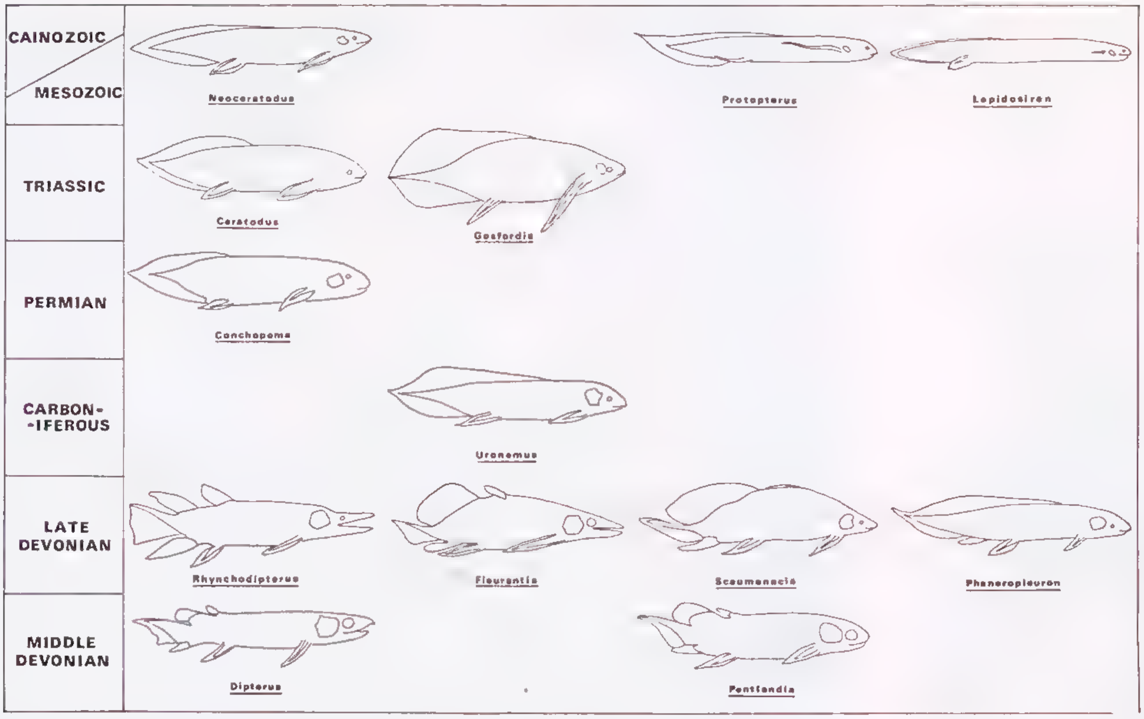

Fig. 3.Outline drawings of representative Dipnoi whose body and fin shapes are well known. All genera reduced to same length for comparative purposes. Stratigraphic ranges and geographical distribution of genera illustrated are as follows:
*Dipterus* Early-Late Devonian; North America, Europe, Asia, Australia.
*Pentlandia* Middle Devonian; Europe.
*Rhynchodipterus* Late Devonian; Europe.
*Fleurantia* Late Devonian; North America.
*Scaumenacia* Late Devonian; North America.
*Phaneropleuron* Late Devonian; Europe.
*Uronemus* Carboniferous; Europe, North America.
*Conchopoma* Carboniferous-Permian; Europe, North America.
*Ceratodus* Triassic-Cretaceous; North America, Europe, Asia, Africa, Australia.
*Gosfordia* Triassic; Australia.
*Neoceratodus* Cretaceous-Recent; Australia.
*Protopterus* Eocene-Recent; Africa.
*Lepidosiren* Miocene-Recent; South America.

In addition to the stratigraphic arrangement (for convenience the Triassic has been considered separately from the rest of the Mesozoic) the 13 genera figured here are also arranged (from left to right) to illustrate the range of "conservative" to "progressive" body forms displayed by dipnoans of approximately the same geological age. No phyletic relationships are implied (redrawn after Jarvik, Lehman, Thomson and others).

# PLATYBRANCH SPHAEROMATIDS (CRUSTACEA: ISOPODA) FROM THE AUSTRALIAN REGION WITH DESCRIPTION OF A NEW GENUS

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## SUMMARY

Recent sampling off the eastern and south-eastern coasts of Australia has produced a number of specimens of platybranchiate sphaeromatid isopods, but the unfortunate lack of detailed keys has led to a number of misidentifications and the curation of unidentified material in museum collections. In an effort to prevent this, all known Australian platybranch species are redescribed and refigured here. The geographical ranges of *Paracassidina pectinata* Baker and *Syncassidina aestuaria* Baker are extended from Western Australia to south-eastern Australia and Queensland. The general biology of *P. pectinata* is discussed and adults of *S. aestuaria* are described for the first time. In addition, a new species, forming a new genus, *Platysphaera membranata* gen. nov., sp. nov., is described from the Coral Sea. A key for the identification of all known Australian platybranchs is provided.

## INTRODUCTION

Survey work involving the sampling of benthic macrofauna off the Queensland coast of Australia is uncovering numerous marine invertebrate species, many of which are new to science and others which have only infrequently been recorded. Unfortunately, due to the lack of detailed keys to many of the common groups, a large number of specimens are not identified and after coding are stored in museum collections (Queensland Museum, 1974a & b; Stephenson and Cook, 1977). This is often the case with crustacean orders such as the Isopoda and Tanaidacea. This paper is one of a series intended to help survey workers and ecologists identify isopods and tanaids from various environments in Australia.

Sphaeromatid isopods are a common element of the marine fauna of the southern hemisphere (Hurley and Jansen, 1977) but little work has been carried out on species not considered to be of economic importance. Hansen (1905) devised a system for sub-dividing the Sphaeromatidae and although it is sometimes difficult to assign newly discovered species to these groups, his system is adhered to in the present paper. Most sphaeromatids belong to two sub-families: the Hemibranchiatinae, in which only the endopods of pleopods 4 and 5 have respiratory folds e.g. *Sphaeroma* Latreille; and the Eubranchiatinae, in which both rami of these appendages have respiratory folds e.g. *Dynamenella* Hansen. A third sub-family, the Platybranchiatinae, in which both rami of pleopods 4 and 5 lack respiratory folds, contains far fewer species and in Australian waters has previously only been represented by the genera; *Chitonopsis* Whitelegge, *Paracassidina* Baker, *Waiteolana* Baker and *Syncassidina* Baker. Very few records exist for these genera and none has previously been recorded off the Queensland coast.

Records of The Australian Museum, 1981, **Vol. 33 No. 12,** 617-643, Figures 1-10.

*Paracassidina* was erected in 1911 by Baker to contain the species *P. pectinata*, collected in Geographe Bay in Western Australia. *Syncassidina* was erected in 1929 by Baker to contain the species *S. aestuaria* from Rocky Bay, Swan River, Western Australia, and only non-ovigerous females were described. These two species have only previously been recorded in their original descriptions, but in the present paper they are recorded from Queensland waters. In addition *S. aestuaria* is recorded from Victoria and *P. pectinata* from Tasmania and New South Wales. Adult specimens of *S. aestuaria* are described for the first time here, and the availability of a relatively large number of specimens of *P. pectinata* has facilitated observations on its general biology.

The only other platybranch species previously known from Australian waters are; *Chitonopsis spatulifrons* Whitelegge, from New South Wales and South Australia, *Chitonopsis hanseni* Nierstrasz, from Indonesian waters, and *Waiteolana rugosa* Baker, from New South Wales, but the present paper contains the description of a new platybranch genus, *Platysphaera*, erected here to house a new species *Platysphaera membranata*, found associated with coral reefs in the Central Coral Sea.

All material not designated a museum location has been placed in a reference collection at Nottingham University.

Fig. 1 shows the known distribution of platybranchiate sphaeromatids in Australian and New Zealand waters.

## SYSTEMATICS

### Order Isopoda

### Family **Sphaeromatidae**

### Subfamily **Platybranchiatinae**

### KEY TO SPECIES FROM THE AUSTRALIAN REGION

1. Body deeply vaulted with entire dorsal surface ornately sculptured (fig. 7)
................................................................................ *Waiteolana rugosa* Baker
— Body flattened, or if vaulted, dorsal surface smooth .................................... 2

2. Epistome visible between expanded antennules in dorsal view .................... 3
— Epistome not visible in dorsal view (fig. 8)
......................................................*Platysphaera membranata*. gen. nov., sp. nov.

3. Epistome extending anteriorly at least as far as anterior margin of antennular peduncle. All pereopods ambulatory, unmodified ......................... 4
— Epistome extending, at most, half way to anterior margin of antennular peduncle. First pereopods highly modified, scythe-shaped (Figs 2,3)
..............................................................................*Paracassidina pectinata* Baker

4. Exopod of uropod minute, not obvious. Pleonal tergite not marked by sutures
(Fig. 4) ..................................................................... *Syncassidina aestuaria* Baker
— Exopod of uropod obvious. Pleonal tergite marked by sutures (Figs 5,6)
............................................................... *Chitonopsis spatulifrons* Whitelegge

5. Merus of pereopod 1 with superior setae very short (Fig. 5)
............................................................... *Chitonopsis spatulifrons* Whitelegge
— Merus of pereopod 1 with superior setae reaching dactylus (Fig. 6)
..........................................................................*Chitonopsis hanseni* Nierstrasz

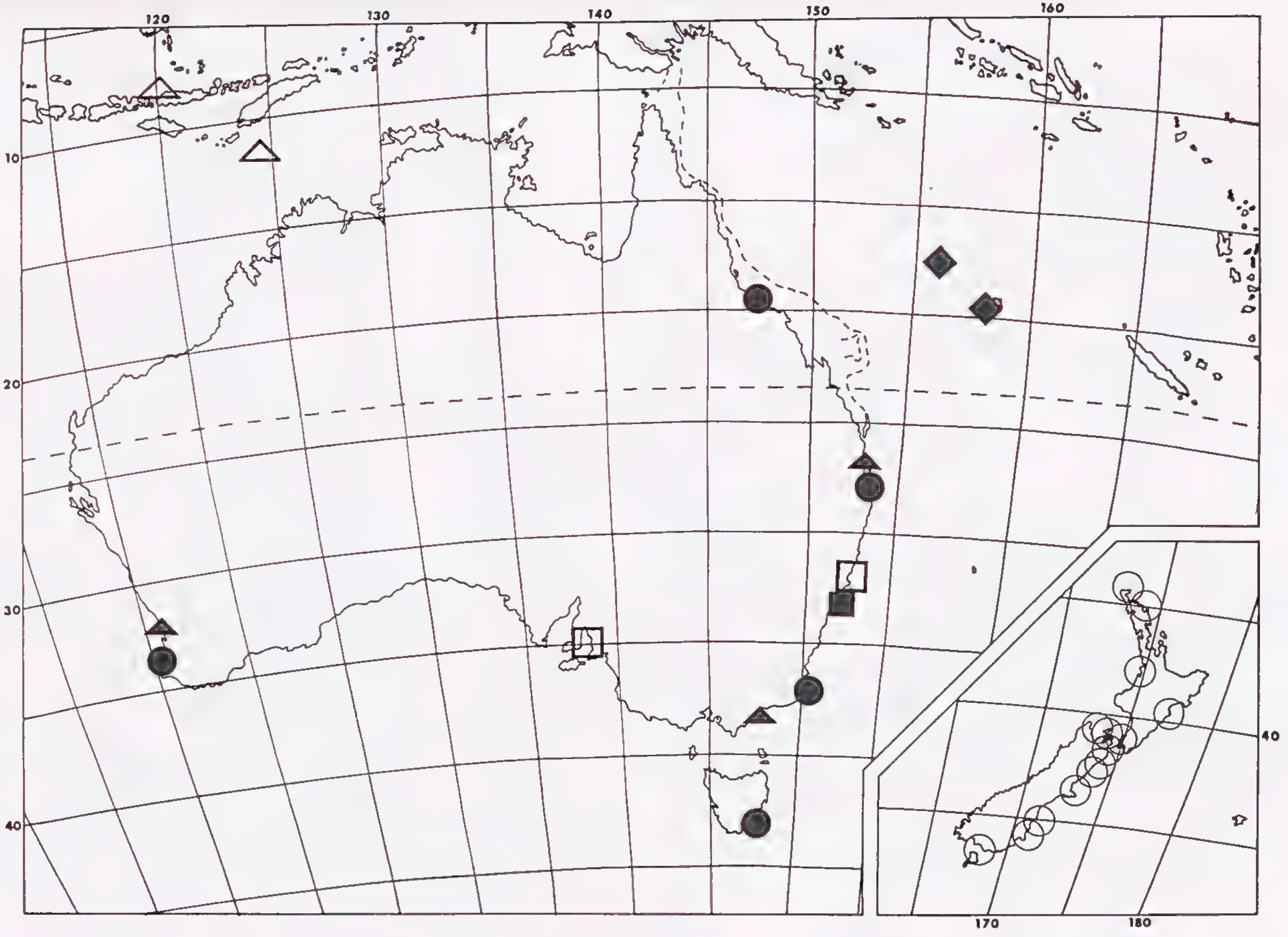

Figure 1. Known distribution of platybranchiate sphaeromatids in the Australia region.

| | | |
|---|---|---|
| ● — *P. pectinata.* | ▲ — *S. aestuaria.* | ■ — *W. rugosa.* |
| ○ — *C. typa.* | △ — *C. hanseni.* | □ — *C. spatulifrons.* |
| ◆ — *Platysphaera membranata* gen. nov., sp. nov. | | |

### Genus **Paracassidina** Baker, 1911

*Paracassidina* Baker, 1911: 90-93, pl. 23. Nierstrasz, 1931: 219.

Type species — *P. pectinata* Baker, 1911.

GENERIC DIAGNOSIS: Body moderately flattened, dorsally naked, punctate, lacking tubercles and projections. Coxal plates of pereonites 2 to 7 separated from tergites by sutures. Pleonal tergite of three segments, fused in midline; anterior not reaching lateral margins of body. Pleotelson with apex entire, lacking notch or groove. Antennular peduncle articles 1 and 2 expanded as flattened lobes projecting anteriorly and laterally. Antennules separated in mid-line by anteriorly produced epistome. Pereopod 1 highly modified, scythe-shaped with long meral lobe; distal articles bearing long setae. Exopod of pleopod 3 with marked line of articulation; both rami with margin of plumose setae. Uropod with minute exopod in outer margin. Sexual dimorphism apparent in antennule form. *Adult male*. Penes separate to base. Appendix masculina present, linear with smoothly rounded apex; arising from proximal, internal angle of endopod of pleopod 2 and extending beyond both rami. Antennular peduncle article 1 markedly bilobed anteriorly with a deep cleft. *Ovigerous female*. Mouthparts not metamorphosed. Brood pouch of three pairs of overlapping brood plates, arising from pereonites 2 to 4, and a posterior pocket. Antennular peduncle article 1 not markedly bilobed anteriorly, lacking a deep cleft.

### **Paracassidina pectinata** Baker, 1911

*Paracassidina pectinata* Baker, 1911:90-93, pl. 23. Nierstrasz, 1931:219.

PREVIOUS RECORDS: Geographe Bay, W.A. (Baker, 1911), 1 male and 1 ovigerous female.

HOLOTYPE: South Australian Museum Reg. No. C 381.

TYPE LOCALITY: Geographe Bay, Western Australia.

MATERIAL EXAMINED: Geographe Bay, W.A.; dredged, 16-20 fms (29-37 m); 1 male, 1 female (with brood plates but no obvious brood) (types); coll. Verco and Torr; South Australian Museum Reg. No. C 381.

Off Twofold Bay, N.S.W. (37°05'S. 150°05'E); sand and mud at 30-50 fms (55-91 m); 1 ovigerous female, 1 non-ovigerous female; coll. Th. Mortensen ("Endeavour"), 30 September 1914; Copenhagen University Zoology Museum (no Reg. No.).

Federick Henry Bay, S.E. Tasmania; 1 male, 2 non-ovigerous females; coll. J. R. Penprase, 16 August 1971; Tasmanian Museum Reg. No. G. 1797.

Middle Banks, Moreton Bay, Qld.; sand and shell, 6-24 m; 26 males, 26 females; coll. Cook and Newlands, 1972-1976; Queensland Museum Reg. Nos. W. 6273-6287.

Bowling Green Bay, Townsville, Qld; sand, muddy sand, 1.9-6.0 m; 2 males, 5 females; coll. P. Arnold, 1974-1975.

Cleveland Bay, Townsville, Qld.; soft mud on shell/mud, 8.9 m; 6 males, 6 females; coll. P. Arnold, 1975.

#### DESCRIPTION OF SPECIMENS FROM QUEENSLAND

Adult male. Body length 3.28 mm. (Figs 2a-m, 3j-l, p, q; Fig. 10).

Body elliptical, twice as long as wide; moderately flattened, coxal plates directed

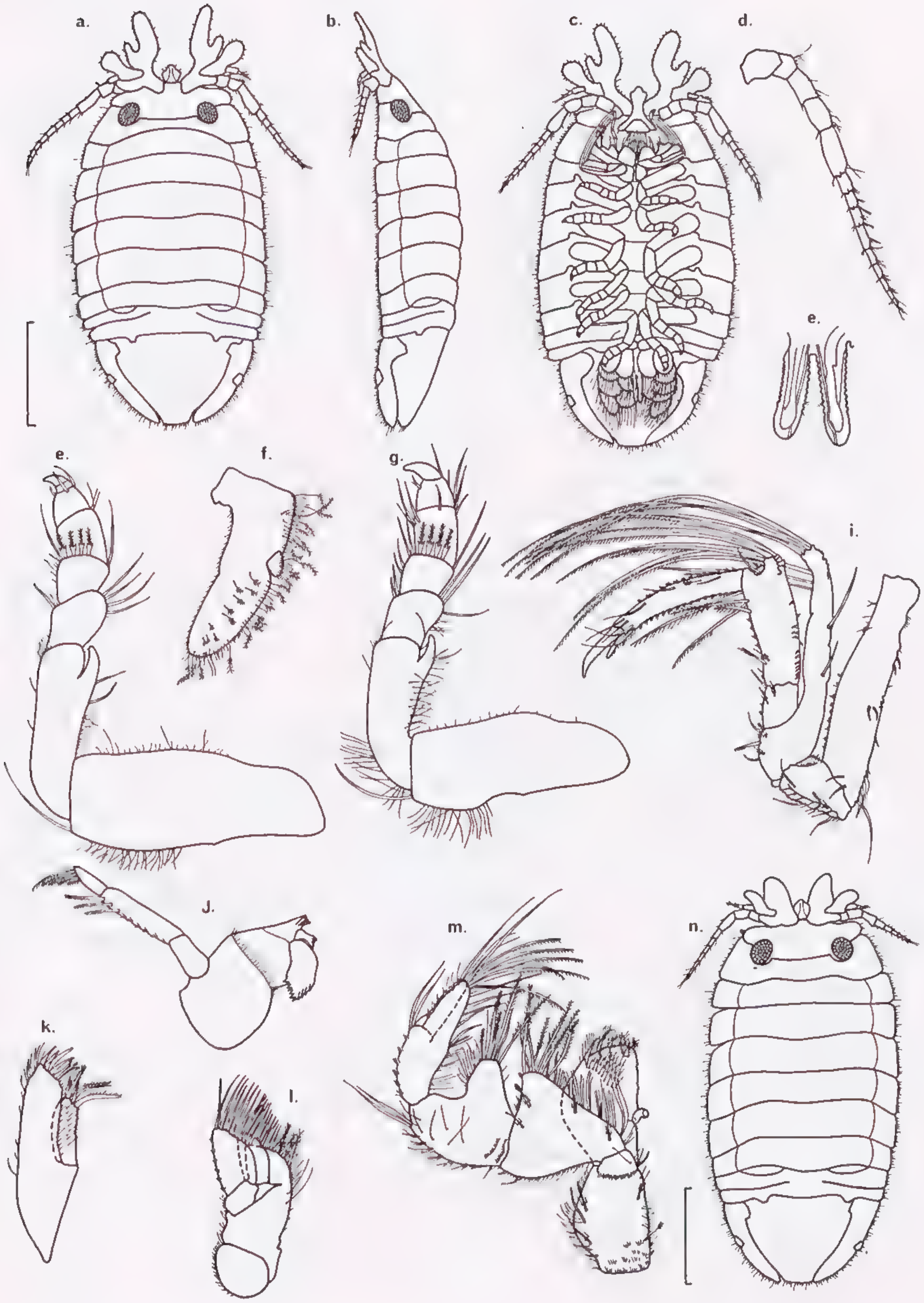

Figure 2. *Paracassidina pectinata* Baker from Queensland. Adult male **(a)** dorsal; **(b)** lateral; **(c)** ventral; **(d)** antenna; **(e)** penes; **(f)** pereopod 6; **(g)** uropod; **(h)** pereopod 2; **(i)** pereopod 1; **(j)** left mandible; **(k)** maxillule; **(l)** maxilla; **(m)** maxillipede. Ovigerous female **(n)** dorsal. Scale line represents 1 mm in each case.

laterally; dorsal surface naked, punctate, lateral margins bearing compound fringing setae. Cephalosome five times as broad as long, having an anterior quadratic projection in mid-line contiguous distally with the tip of the anteriorly produced epistome. Laterally, division between cephalosome and pereonite 1 lying anterior to eyes, which are well developed, darkly pigmented and set posteriorly into the anterolateral margin of pereonite 1. Lateral margins of pereonites and pleonal tergite closely applied forming a regular, sub-continuous outline. Pleotelson sub-triangular with apex broadly truncated.

*Antennae*. Antennular peduncle article 1 strongly flattened and produced into lobes; a larger, bifid, inner lobe projecting anteriorly, and an outer lobe projecting laterally (Fig. 10). Article 2 also flattened, anteriorly extended, arising from an excavation between the lobes of article 1; 3 cylindrical, arising mid-way along external margin of article 2. Flagellum of three articles, distal two each bearing one aesthetasc. Antennal articles not expanded; nine-articled flagellum reaching level of pereonite 4. *Mouthparts*. Epistome produced anteriorly beyond cephalosome, widening distally as a short process, visible between antennules in dorsal view; ventral, proximal region embracing labrum. Mandible with quadridentate incisor process; molar process well developed, strongly dentate; palp well developed, article 2 with three, and article 3 with five, pectinate setae; lacinia mobilis of left mandible as a quadridentate peg. Maxillule with ten simple spines on exopod, two simple spines and four pectinate spines on endopod. Maxilla with long, simple spines on both outer lobes and shorter, more robust, plumose spines on the inner lobe. Maxillipede with palp articles 2 to 4 strongly lobed, 5 extending only as far as tip of lobe of article 4. *Pereopods*. Pereopod 1 highly modified, held horizontally across the mouthparts. Basis long, slender, directed medially; ischium very short; merus extended superiorly as an elongated lobe running alongside the propus; carpus short; propus well developed and widening distally; dactylus long, arising from inferior border of propus and held at right angles to it; unguis well developed, one third length of dactylus, with an inferior, basal spine. Apex of meral lobe with four very long, curved setae, each pectinate in distal half; distal, inferior margin of lobe with three similar setae and one shorter simple seta near apex. Distal tip of propus with a number of longe setae, pectinate in distal half; inferior margin with two pectinate and two plumose setae. All long setae mentioned above projecting inferiorly at right angles to meral lobe and in same plane as elongated dactylus. Pereopods 2 to 7 ambulatory, similar in form, moderately setose; basis expanded for distal one third of length; ischium with superior hooked protuberance; merus with superior distal lobe; carpus with four distal, trifid, plumose spines; dactylus with strongly curved unguis. *Penes* short, reaching just beyond articulation of basis of pleopod 1 and pleonal tergite. *Pleopods*. Pleopod 1 with exopod and endopod sub-similar, each with terminal plumose setae sub-equal in length to ramus bearing them. Exopod also bearing external plumose setae. Pleopod 2 with endopod more rectangular than slightly larger exopod, inner margin of endopod with well developed appendix masculina — one and a half times length of ramus. Setation as in pleopod 1. Pleopod 3 with endopod rectangular and slightly larger than ovate, two-articled exopod. Each ramus with terminal plumose setae half length of ramus, and exopod with similar external setae. Pleopods 4 and 5 with both rami lacking respiratory folds; blood lacunae obvious; proximal inner regions thickened; exopods larger than endopods. Exopod of 5 with three equidistant finely-toothed bosses in distal half of inner margin and several short, simple setae on external border. *Uropods*. Endopod juxtaposed to pleotelsonic margin, terminating just before apex. Exopod minute, housed in notch in proximal one third of lateral margin.

Ovigerous female. Body length 3.78 mm. (Fig. 2n).

Similar to male excepting primary sexual characteristics and form of antennular peduncle. Peduncle articles 1 and 2 as dorsoventrally flattened lobes, but anteriorly

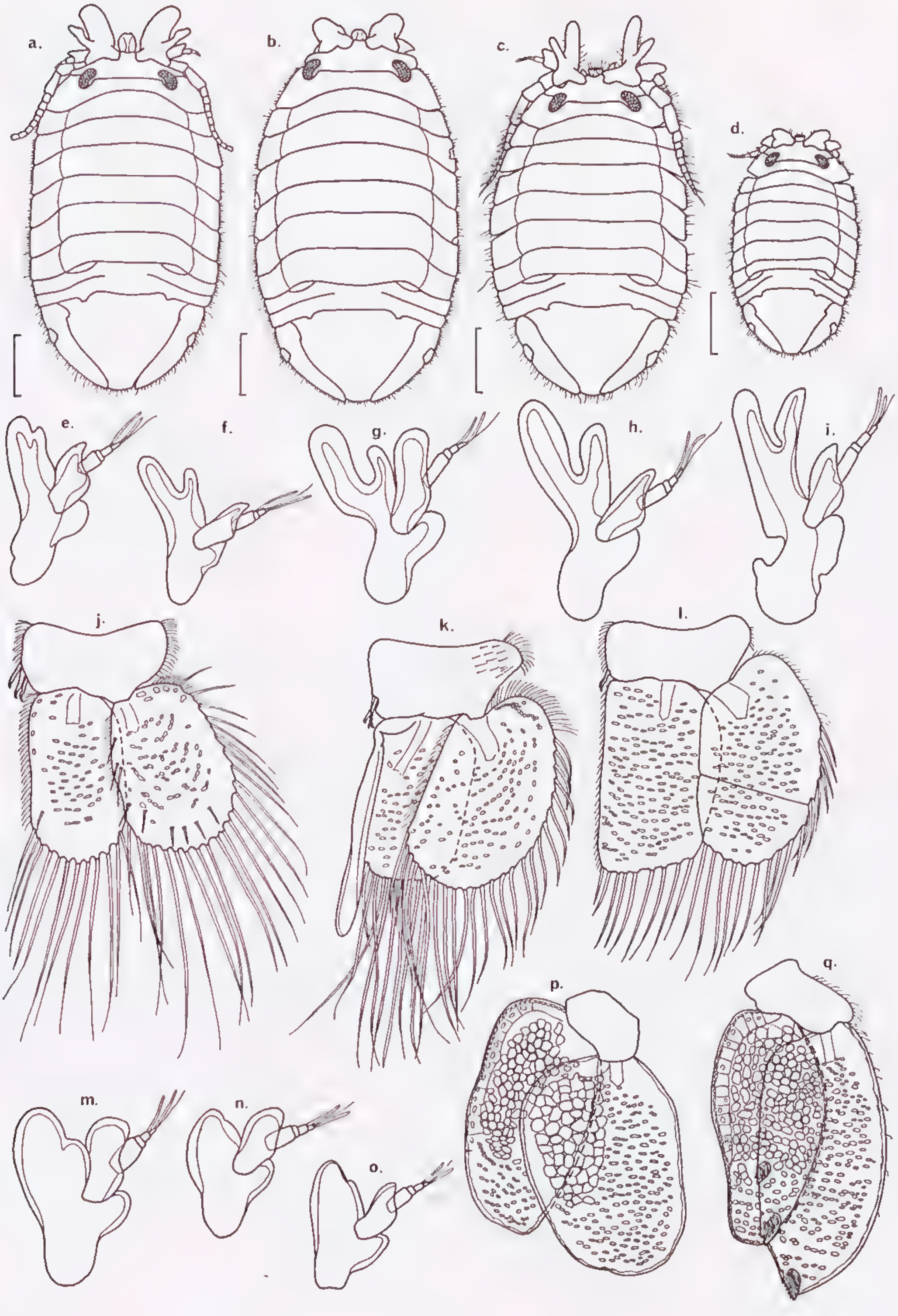

Figure 3. *P. pectinata* Baker. **(a)** adult male (type) — dorsal; **(b)** ovigerous female (type) — dorsal; **(c)** adult male from Tasmania — dorsal; **(d)** non-ovigerous female from Tasmania — dorsal. Queensland specimens. Adult males **(e)** to **(i)** antennules; **(j)** to **(i)**, **(p)**, **(q)** pleopods 1 to 5 respectively (setules omitted from plumose setae). Ovigerous females **(m)** to **(o)** antennules. Scale line represents 1 mm in each case.

projecting lobe of 1 is single and relatively shorter than in male. Brood pouch formed from three pairs of brood plates, increasing in size posteriorly and arising from pereonites 2-4, those on pereonite 4 being three times the size of those on pereonite 3 and nine times the size of those on pereonite 2. In addition to the brood plates there is an anteriorly directed pocket covering the posterior sternite and opening between the seventh pereopods. Mouthparts unmodified.

Non-ovigerous female:

As above but without the brood pouch.

INTRASPECIFIC VARIATION: In addition to the gross sexual differences in the form of the antennular peduncle, the Queensland specimens also show variation in this character within each sex (Fig. 3e-i, m-o). This variation between sexes and between individuals of the same sex is important to bear in mind when considering the formation of new species based on minor characters. The Queensland specimens do differ slightly in the form of epistome tip from the type specimens (Fig. 3a, b) and specimens from Tasmanian waters (Fig. 3c, d) but due to the geographical separation of the three localities, the variation shown by the antennules of the Queensland specimens, and the similarity of all specimens in all other respects, their separation as distinct species would be unjustified. Morphological variation with geographical location has also been noted in the *Serolis minuta*-group, isopods which are found in similar habitats to *P. pectinata* (Holdich and Harrison, in press (a)).

Amongst the specimens from Queensland one male was found with the male antennular form, appendices masculinae and penes, but also with fully formed brood plates, although the posterior pocket was not developed.

REMARKS: Although *Paracassidina* bears a superficial resemblance to *Chitonopsis* there are marked differences, notably the highly modified first pereopod, and the antennular peduncle extending anteriorly well beyond the epistome tip.

Regarding the variation in form of the epistome tip of *P. pectinata:* if a gradual change from the form found in the type specimens (Fig. 3a, b) to the form found in the Tasmanian specimens (Fig. 3c, d) is anticipated, the Queensland and New South Wales specimens form intermediates, suggesting that the range of this species may extend around the north coast of Australia and down the east coast to Tasmania rather than following the south coast. Unfortunately there is no evidence to suggest this gradual change with geographical location, and more sampling must be carried out before the true range of this species can be appreciated. It is interesting to note, however, that *P. pectinata* has not been recorded during intensive sampling of the Port Phillip Bay area (Naylor, 1966; Poore *et al.,* 1975) where depth and substratum are similar to those in its known sites.

PARASITES: The intersex male mentioned above was also found to have the cryptoniscan stage of an epicaridian isopod parasite in its "brood pouch". A number of ovigerous females were also found with cryptoniscid and other stages of development of (presumably) this parasite. As many parasites evolve with their host and a number of epicaridian isopods are believed to be species specific, although the evidence is not conclusive (Schultz, 1969: 338; Nielsen and Stromberg, 1973: 76), it is possible that the epicarid mentioned here is a new species.

## ECOLOGY AND BREEDING BIOLOGY IN QUEENSLAND WATERS

Specimens of *P. pectinata* were collected during routine sampling of the fauna associated with particulate substrata in various bays in Queensland. The Townsville samples were collected during the James Cook University Three Bays Survey using a modified Barnett-Hardy suction sampler with a 1mm or 1.5mm mesh bag. The Brisbane samples were collected for Queensland University using a Smith-McIntyre grab. It seems likely that the sampling methods precluded collection of the younger stages of the life-cycle. The adults collected appear to have been associated with either the surface of the sediment or the top few millimetres, and observations of the gut contents revealed only detritus. This observation, coupled with the presence of very highly modified first pereopods, suggests that this isopod may obtain its food from particles sifted from the sediment with this modified limb. Such a method of feeding would be unusual for a sphaeromatid, although Rotramel (1975) has suggested it for *Sphaeroma quoyanum* Milne-Edwards, in which the limbs concerned are not as highly modified as in *P. pectinata.*

*P. pectinata* in Queensland appears to be associated with a variety of particulate substrata, ranging from fine mud to sand with shell gravel at depths from approximately 2m to 24m. Ovigerous females were taken in most samples and breeding appears to occur all the year round, a situation typical of shallow water populations in sub-tropical and tropical marine habitats. Large numbers of other invertebrate species were to be found in the same samples as *P. pectinata,* notably polychaete annelids (P. Arnold, personal communication) and a number of other isopod groups e.g. anthurids, cirolanids, small serolids and gnathiids. The systematics and some aspects of the ecology of the last two groups have been dealt with by Holdich and Harrison (in press (a) and (b)). The serolids at least would appear to occupy a similar niche to *P. pectinata,* although the food taken is probably of larger dimensions. Specimens from New South Wales were also taken in association with serolids but from a greater depth i.e. 91m.

### Genus **Syncassidina** Baker, 1929

*Syncassidina* Baker, 1929: 60, 61, pl. 5. Nierstrasz, 1931: 222.
Type species — *S. aestuaria* Baker, 1929.

GENERIC DIAGNOSIS: Body moderately flattened, smooth, with a compound setal margin. Coxal plates of pereonites 1 to 7 separated from tergites by sutures. Single pleonal tergite lacking sutures. Pleotelson with apex entire, lacking notch or groove. All tergites reaching lateral margins of body except anterolateral angles of pleotelson. Antennular peduncle articles 1 and 2 expanded as flattened lobes anterior to cephalosome; sub-equal in length to and separated by cuneiform epistome. Pereopods ambulatory, unmodified. Exopod of pleopod 3 lacking articulations; both rami lacking plumose setae. Uropods large with minute exopods set in lateral margins. (Exopods not lacking as stated by Baker, 1929: 60, 61). Secondary sexual dimorphism not apparent. *Adult male.* Penes slender, simple, separate to base. Appendix masculina present, arising from proximal internal angle of endopod of pleopod 2 and extending beyond both rami. *Ovigerous female.* Mouthparts not metamorphosed. Brood pouch formed from an anterior pocket opening at the level of pereopod 3 and a posterior pocket opening at the level of pereopod 4. Pereopods 3 and 4 bearing small brood plates not overlapping in the ventral mid-line.

### **Syncassidina aestuaria** Baker, 1929

*Syncassidina aestauria* Baker, 1929: 60, 61, pl. 5. Nierstrasz, 1931: 222.
*Chitonopsis* sp. — Queensland Museum, 1974a: 9. Queensland Museum, 1974b: App. 1, p. 2; App. 2, pp. 2, 5, 8, 14, 17, 20, 23.

PREVIOUS RECORDS: Rocky Bay, Swan River, W.A. (Baker, 1929), non-ovigerous female.

HOLOTYPE: Western Australian Museum Reg. No. 11180 (4 microslides).

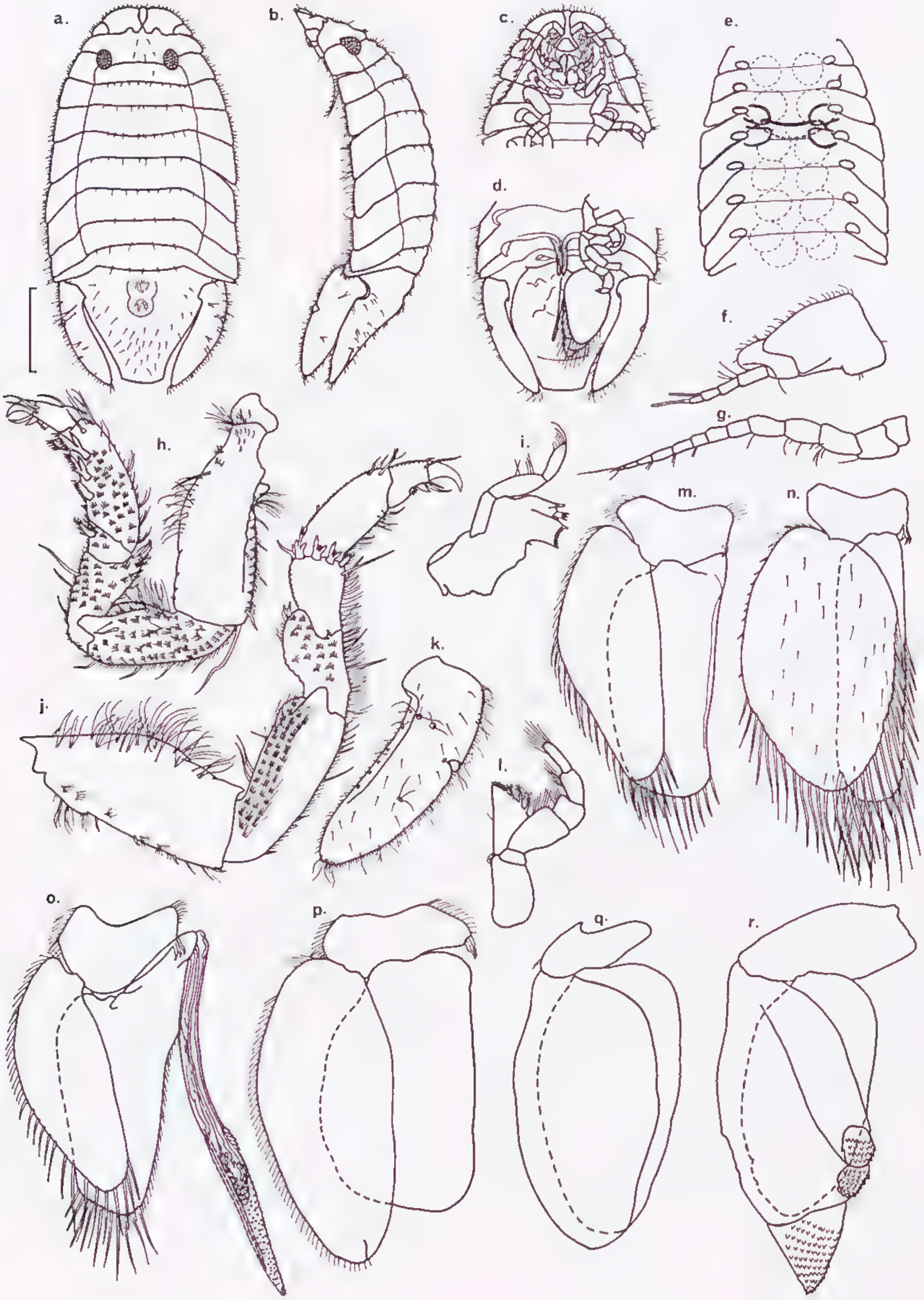

Figure 4. *Syncassidina aestuaria* Baker. Adult male **(a)** dorsal; **(b)** lateral; **(c)** ventral anterior; **(d)** ventral posterior, right pleopods removed; **(f)** antennule; **(g)** antenna; **(h)** pereopod 1; **(i)** left mandible; **(j)** pereopod 2; **(k)** uropod; **(l)** maxillipede; **(n)** to **(r)** pleopods 1 to 5 respectively (blood lacunae and setules of plumose setae omitted). Ovigerous female **(e)** ventral pereon showing brood pouch opening and position of ova; **(m)** pleopod 2 (lacunae and setules omitted). Scale represents 1 mm.

TYPE LOCALITY: Rocky Bay, Swan River, Western Australia.

MATERIAL EXAMINED: Rocky Bay, Swan River, W.A.; 1 non-ovigerous female (type); coll. L. G. Glauert; Western Australian Museum Reg. No. 11180.

Caboolture River, S.E. Queensland; 1 km up Tributary Creek, 4.5 km from mouth; 2 non-ovigerous females; coll. Coastal Management Survey, 23 May 1974; Queensland Museum Reg. No. W. 5611.

Serpentine Creek, S. E. Queensland; right bank 4.5 km in from mouth, Site 4/R, sample 153; 1 non-ovigerous female; coll. B. Campbell *et al.*, 20 February 1973; Queensland Museum Reg. No. W. 4323.

East of Swan Bay, S. Moreton Bay, S. E. Queensland; Mangrove Patch; 1 male; coll. P. Shanco, 18 May 1976; Queensland Museum Reg. No. W. 6305.

Banksia Peninsula, Gippsland Lakes, Victoria; from *Zostera* community, depth 1m; 3 ovigerous females, 5 non-ovigerous females, 2 juveniles; coll. G. C. B. Poore, 30 November 1978.

## DESCRIPTION OF SPECIMENS FROM QUEENSLAND

Adult male. Body length 4.23 mm (Fig. 4a-d, f-l, n-r)

Body with subcontinuous, elliptical outline; twice as long as wide; moderately flattened with coxal plates directed laterally; surface smooth. Cephalosome four times as wide as long with an acute anterior projection in mid-line lying between two blunt projections on anterior margin.

Antennular peduncle articles 1 and 2 forming smooth, arcuate anterior margin; separated in dorsal view by cuneiform epistome extending anteriorly to limit of article 1. Pleotelson convex, bearing two low, setose tubercles in the anterior mid-line.

*Antennae.* Antennular penduncle articles 1 and 2 flattened, 1 approximately four times the size of 2; 3 cylindrical. Flagellum of four articles, last two each bearing a single aesthetasc. Antennal peduncle article 1 reduced, 2 to 5 sub-equal. Flagellum of eight articles. *Mouthparts.* Labrum broad, deeply set into base of anteriorly produced epistome. Mandibles with incisor processes, molar processes and palps well developed. Lacinia mobilis of left mandible as a tridentate peg; right mandible with row of spines. Maxillule and maxilla of usual sphaeromatid form. Maxillipede with palp articles narrow, 2 as long as 3 and 4 together; 2 to 4 with weakly produced setigerous lobes, 5 with apical setae. *Pereopods.* Ambulatory, increasing in size posteriorly to 5, then 6 and 7 decreasing. Pereopod 1 with carpus reduced and inferior margin of propus bearing three strong pectinate spines, the distal two being bifid. Distal margin of carpus of pereopods 2 to 7 bearing a row of trifid spines. Dactylus of all pereopods with a strong simple setae opposing the unguis, giving a chelate appearance, and a small secondary unguis. *Penes.* Simple, six times as long as broad, separate to base. *Pleopods.* Rami of pleopod 1 sub-equal in length, endopod rectangular, four times as long as wide; exopod ovate, two and a half times as wide as endopod. Both rami bearing short internal and terminal plumose setae and a number of short, simple, non-marginal setae. Endopod of pleopod 2 trapezoidal with apical row of short plumose setae and an inner appendix masculina one and a half times the length of the ramus and arising from the proximal, internal angle. Appendix masculina widest at its mid-point and covered with small teeth distally. Exopod sub-equal in length to endopod, sub-elliptical, with short, terminal and external plumose setae. Exopod of pleopod 3 sub-elliptical, twice as long as broad with an external fringe of simple setae. Endopod slightly wider than exopod, broadly truncate, lacking setae. Both rami lacking articulations and plumose setae. Rami of pleopod 4 ovate, sub-equal, lacking setae and articulations. Endopod of pleopod 5 elliptical, twice as long as broad. Exopod one and a half times length of endopod, apex acute and separated from proximal three-quarters by an articulation. Apical article finely toothed over entire surface. Proximal article bearing two contiguous, toothed bosses on internal, distal margin. Bosses lying either side of a long oblique fold in the pleopod surface. *Uropods.* Endopods broad, juxtaposed to pleotelsonic margin. Exopods minute, set in external margin two-thirds of the length from the apex.

Ovigerous female. Body length 4.42 mm (Fig. 4e, m).

Similar to male excepting primary sexual characteristics. Brood pouch formed by an anterior pocket extending from the cephalosome to the level of pereopod 3, and a posterior pocket extending from the level of the pleopods to the level of pereopod 4. These opposing pockets open between the third and fourth pereopods, the smoothly rounded lip of the anterior pocket being well overlapped by the bi-lobed lip of the posterior (Fig. 4e). The remaining lateral openings are each covered by a pair of small brood plates, arising from pereopods 3 and 4. Within this brood pouch the ova are embedded in the ventral surface of the body, either side of the nerve cord, some ova lying against the terga and being visible through the cuticle in dorsal view. The brood pouch of one female examined contained 23 ova. Mouthparts unmodified.

REMARKS: Morton and Miller (1968: 214, 403-4) mentioned an unidentified isopod from New Zealand which they called *Chitonopsis* sp. Their diagram of this isopod, however, bears a much greater resemblance to *Syncassidina* than to *Chitonopsis*, and its habitat, under stones in stream mouths, a brackish site, would tend to reinforce the view that this is a species of *Syncassidina*. Unfortunately, no full description has been published and the original specimens are no longer available (Hurley and Jansen, 1977: 26). At present the only known platybranch from New Zealand is *Cassidina typa* M-Edw., which is not known from Australian waters (see Fig. 1) and the discovery of a *Syncassidina* species from New Zealand, giving these two regions a common platybranch genus, would be most interesting.

### Genus **Chitonopsis** Whitelegge, 1902

*Chitonopsis* Whitelegge, 1902: 278-283. Hale, 1929: 305. Nierstrasz, 1931: 219-221.
*Chitinopsis* — Hansen, 1905: 83, 112, 131, *(lapsus calami).*
Type species — *C. spatulifrons* Whitelegge, 1902.

GENERIC DIAGNOSIS: Body elliptical, smooth. Coxal plates of pereonites 2 to 7 separated from tergites by sutures. Pleonal tergite of three apparent segments, fused in mid line, anterior not reaching lateral margins of body. Pleotelson smoothly convex, lacking projections, with apex entire, lacking notch or groove. Antennular peduncle articles 1 and 2 expanded as dorsoventrally flattened lobes, separated in mid-line by anteriorly produced epistome. Epistome extending at least to anterior tip of first peduncle article of antennule. All pereopods ambulatory, unmodified. Exopod of uropod reduced, housed in notch in external margin. *Adult male.* Penes separate to base. Appendix masculina present, having a blunt, dilated tip and arising from proximal, internal angle of endopod of pleopod 2 and extending beyond both rami. *Ovigerous female.* Brood pouch formed from four pairs of brood plates arising from pereopods 1 to 4. Mouthparts not metamorphosed.

### **Chitonopsis spatulifrons** Whitelegge, 1902

*Chitonopsis spatulifrons* Whitelegge, 1902: 278-283. Hansen, 1905: 83, 112, 131. Hale, 1929: 305-6. Nierstrasz, 1931: 221.

PREVIOUS RECORDS: Off Port Jackson, Coogee and Crookhaven River, N.S.W. (Whitelegge, 1902).

SYNTYPES: Australian Museum Reg. Nos. G. 2151-2 ( +1?).

TYPE LOCALITIES: Off Port Jackson, Coogee and Crookhaven River, N.S.W.

MATERIAL EXAMINED: Off Port Jackson, N.S.W.; trawled 2.5 to 3.5 miles (4-5.6 km) from shore, sand and mud, depth 36-39 fathoms (66-71 m); 1 male (syntype); coll. E. R. Waite, 10 March 1898 ("Thetis" Expedition Station 34); Australian Museum Reg. No. G. 2151.

Off Coogee, N.S.W; trawled 5-6 miles (8-9.7 km) from shore, fine sand, depth 49-50 fathoms (89-91 m); 1 ovigerous female (syntype); coll. E. R. Waite, 15 March 1898 ("Thetis" Expedition Station 44); Australian Museum Reg. No. G. 2152.

St. Vincent Gulf, South Australia; 4 fathoms (7.3 m); 1 male; coll. H. M. Hale; South Australian Museum Reg. No. C. 1057.

St. Vincent Gulf, South Australia; dredged, 18 fathoms (33 m); 1 male; coll. H. M. Hale, 2 February 1924; South Australian Museum Reg. No. C. 1557.

St. Vincent Gulf, South Australia; 1 male, 1 damaged specimen; coll. W. H. Baker; South Australian Museum Reg. No. C. 577.

St. Vincent Gulf, South Australia; 5 males, 5 ovigerous females; South Australian Museum.

Locality unknown; dredged; 1 non-ovigerous female; coll. Verco; South Australian Museum.

SPECIFIC DESCRIPTION: Adult male. Body length 9.8 mm (Fig. 5)

Body elliptical, slightly more than one and a half times as long as wide, very depressed, smooth, lacking projections and dorsal setae, bearing marginal fringe of short setae. Cephalosome four times as wide as long with anterior quadratic projection in mid-line, contiguous with epistome. Eyes small, reniform and — with median region of cephalosome — set into tergum of pereonite 1. Dorsally visible region of epistome and antennular peduncle article 1 equal in length to cephalosome. Pereonal tergites 1 to 7 sub-equal in length with well formed laterally directed coxal plates, those of pereonites 2 to 7 separated from the tergites by sutures. Pleotelson sub-triangular, antero-lateral angles not reaching lateral margins of body; apex smoothly rounded.

*Antennae*. Antennular peduncle with article 1 directed anteriorly, sub-rectangular, one and a half times as long as broad, with an external notch housing article 3. Article 3 half length of 2, cylindrical and bearing six-articled flagellum. Antenna with peduncle article 1 reduced, 2 to 5 sub-equal, 1 to 5 setose on superior margin, 3 to 5 setose on inferior margin. Setose flagellum of 14 articles. *Mouthparts*. Epistome sub-rectangular with distal lateral margins parallel, expanding proximally to enclose labrum. Mandibles with quadridentate incisor processes and well developed, dorsally acute, molar processes. Inferior borders of palp articles 2 and 3 bearing many plumose setae. Lacinia mobilis of left mandible as a stout, tridentate peg next to four pectinate spines. Right mandible with a cluster of simple spines only. Maxillule and maxilla of usual sphaeromatid form. Maxillipede with palp very well developed. Palp article 1 reduced, 2, 3 and 4 sub-equal, bearing pronounced lobes with apical, plumose setae. *Pereopods*. All ambulatory, unmodified. Pereopod 1 more slender than succeeding; carpus reduced; propus elongate, three and a half times as long as broad; inferior margins of merus,

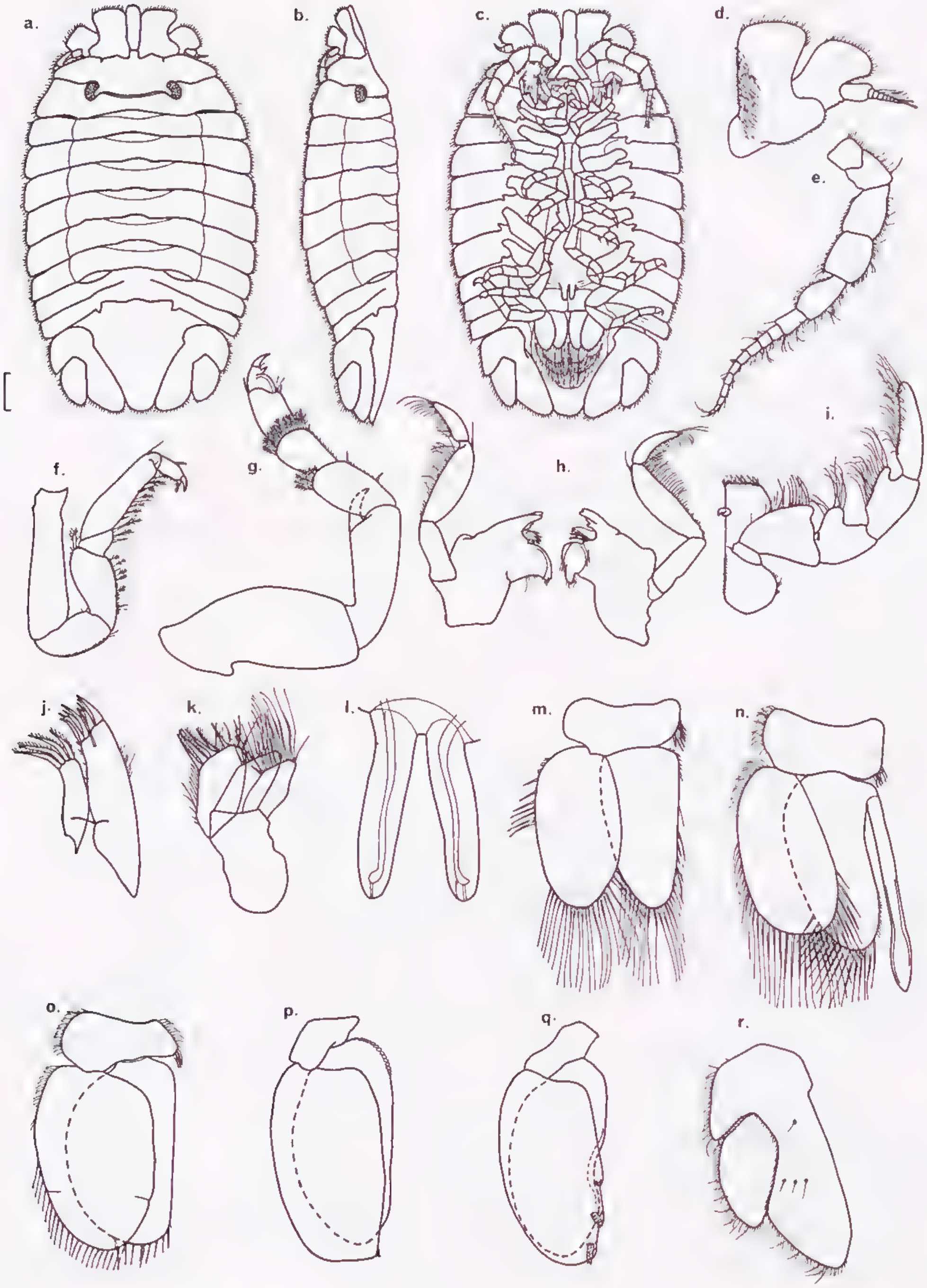

Figure 5. *Chitonopsis spatulifrons* Whitelegge. Adult male **(a)** dorsal (type); **(b)** lateral (type); **(c)** ventral (type); **(d)** antennule; **(e)** antenna; **(f)** pereopod 1; **(g)** pereopod 4; **(h)** mandibles; **(i)** maxillipede; (j) maxillule; **(k)** maxilla; **(l)** penes; **(m)** to **(q)** pleopods 1 to 5 respectively (blood lacunae and setules of plumose setae omitted); **(r)** uropod. Scale line represents 1 mm.

carpus and propus bearing many stout plumose setae. Superior distal lobe of merus with one such seta. Pereopods 2 to 7 similar; ischium bearing curved, distal, antero-superior projection; superior distal lobe of merus and posterior distal margin of carpus with row of plumose setae; dactylus robust with strong unguis and small secondary unguis. *Penes.* Simple, each five times as long as wide, cylindrical, with a hemispherical tip. *Pleopods.* Basis of pleopod 1 with seven simple spines on interno-distal margin. Rami sub-equal in length, exopod elliptical, endopod sub-ovate, elongate. Both rami with terminal fringe of long plumose setae. Exopod with external and endopod with internal fringe of long plumose setae. Basis of pleopod 2 with five spines on internal distal margin. Both rami sub-elliptical with terminal, and exopod with external, plumose setae. Endopod slightly narrower and longer than exopod with the internal proximal angle bearing an appendix masculina approximately one and a quarter times the length of the ramus. Appendix masculina twelve times as long as wide with sub-parallel margins and a dilated tip. Basis of pleopod 3 with three spines on the internal distal margin. Rami sub-equal. Exopod bearing very faint sign of an articulation at either side in distal half. Endopod with several, and exopod with many, short, terminal, plumose setae. Rami of pleopod 4 sub-equal, lacking folds, articulations and setae. Proximal, internal margin of endopod with a row of small "scales". Rami of pleopod 5 sub-equal, lacking folds, articulations and setae. Internal, distal margin of exopod bearing three separate, finely-toothed bosses. Inner margin of endopod thickened in region juxtaposed to proximal boss on exopod. *Uropods.* Twice as long as wide. Rounded tip of endopod reaching level of pleotelsonic apex. Exopod half length of endopod, borne in notch on external margin. Outer margins of both rami setose.

Ovigerous female. Body length 13.1 mm.

Similar to male excepting primary sexual characteristics. Brood pouch composed of four pairs of brood plates only, arising from pereonites 1 to 4. Brood plates increasing in size posteriorly and overlapping well in mid-line. Anterior and posterior pockets absent but with the ventral body wall, anterior to the pleopods, dilating ventrally as a shelf juxtaposed to the internal face of the posterior brood plates, the anterior rim of this shelf preventing posterior passage of the eggs. Mouthparts not metamorphosed.

REMARKS: Whitelegge (1902: 283) in describing this species gave the total length of the male as 13 mm and the breadth as 8 mm. Even including the epistome of the present male syntype it does not reach these proportions. It must be concluded therefore that the male specimen to which he refers was larger than the syntype figured here and it was presumably that specimen which was collected off the Crookhaven River, the habitat details being: Off Crookhaven River, N.S.W.; trawled 4 miles (6.4 km) from shore, rock, depth 23 fathoms (42 m); 1 ? male (syntype); coll. E. R. Waite, 19 March 1898 ("Thetis" Expedition Station 53).

Excepting primary sexual characteristics, sexual dimorphism is not apparent in this species. The following morphological comparisons between males (n=9) and ovigerous females (n=6) were made. Mean body length: males 12.57 mm (SD = ± 2.956), females 14.46 mm (SD = ± 1.62). Mean body length/ body width ratio: Males 1.403 (SD = ± 0.104), females 1.405 (SD = ± 0.07). Mean number of antennular flagellum articles: males 7 (SD = ± 1.6), females 7 (SD = ± 1.5). Mean number of antennal flagellum articles: males 12 (SD = ± 1.85), females 13 (SD = ± 1.73).

It was noted, however, that some of the larger individuals bore very slight median and medio-lateral pereonal tubercles.

### **Chitonopsis hanseni** Nierstrasz, 1931*

*Chitonopsis hanseni* Neirstrasz, 1931: 219-221.

RECORDS: Labuan Badjo and Timor Sea, Indonesia.

SYNTYPES: Zoological Museum, Amsterdam Reg. Nos. IS. 100. 617-618.

TYPE LOCALITIES: Labuan Badjo, Flores Sea and Timor Sea (10°12.2′S., 124°27.3′E) Indonesia.

MATERIAL EXAMINED: Labuan Badjo, Flores Sea, Indonesia; depth 27-36 m; 1 male, 1 ovigerous female (syntypes); coll. M. Weber, 16-18 April 1899 (Siboga Expedition Station 50); Zoological Museum, Amsterdam Reg. No. IS. 100. 617.

Timor Sea (10°12.2′S., 124°27.3′E); depth 73 m; 1 sub-adult male (syntype); coll. M. Weber, 23 January 1900 (Siboga Expedition Station 294); Zoological Museum, Amsterdam Reg. No. IS. 100. 618.

SPECIFIC DESCRIPTION: Adult male. Body length 8.4 mm (Fig. 6a, b, d, h-o, u, v).

Body elliptical, two and a half times as long as wide, deeply vaulted, lacking projections and dorsal setae. Cephalosome approximately three times as wide as long with anterior quadratic projection in mid-line, dorsal to epistome, not smoothly contiguous with it. Eyes large, reniform, set into tergum of pereonite 1. First antennular peduncle article one and a half times length of cephalosome, not extending anteriorly as far as tip of epistome. Pereonal tergites 1 to 7 sub-equal in length, with well developed, ventro-laterally directed coxal plates, those of pereonites 2 to 7 separated from the tergites by sutures. Pleotelson sub-triangular, apex truncate.

*Antennae*. Antennular peduncle article 1 directed anteriorly, dorso-ventrally flattened, sub-triangular, apex rounded; 2 sub-pentagonal, extending laterally from article 1; 3 sub-rectangular. Flagellum of eight articles. Antennal peduncle articles not expanded; flagellum of fourteen articles. Antenna reaching posteriorly to pereonite 4. *Mouthparts*. Epistome elongate distally, sub-cylindrical, punctate ventrally, widely bifid proximally enclosing trapeziform labrum and extending anteriorly beyond antennular peduncle article 1. Mandible with well formed palp, tridentate incisor process, setal row and acute molar process. Palp articles 2 and 3 with many plumose setae along inferior margins. Maxillule and maxilla of usual sphaeromatid form. Maxillipedal palp with broad lobe on article 2 and narrow lobes on articles 3 and 4. Articles 2 to 5 with inferior margin of plumose setae. *Pereopods*. Peropod 1 slender with ischium, merus and propus sub-equal in length; carpus reduced; dactylus slender, twice as long as wide; merus with distal superior lobe bearing several long setae which extend to distal margin of propus. Inferior margins of merus, carpus and propus setose. Pereopods 2 to 6 similar, more robust than 1; ischium to propus with each article slightly shorter than that preceding; dactylus robust. Merus with slight superior distal lobe bearing short setae. Superior distal margin of carpus bearing several long setae. Inferior margins of carpus and propus with several setae. Pereopod 7 as for 2 to 6 but inferior margin of carpus bearing a pronounced row of 7 setae. *Penes*. Separate to base, three times as long as wide. *Pleopods*. Missing from specimen; following description based on Nierstrasz (1931: Fig. 128) and reproduced here as Fig. 6V. Pleopod 2 with endopod just longer than elliptical exopod. Proximal internal margin of endopod bearing an appendix masculina longer than the endopod

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*Since going to press a specimen of *C. hanseni* has been sent to the authors from Queensland. The collection details are: Moreton Bay, Qld.; on ascidian, trawled 6 m, 27° 31.4′S 153° 22.2′ E; 1 ovigerous female; coll. N. Bruce and N. Svennivig, 10 July 1979; Q. M. Reg. No. W.8047. This is the first record of this species from the Australian coast and greatly extends its known range.

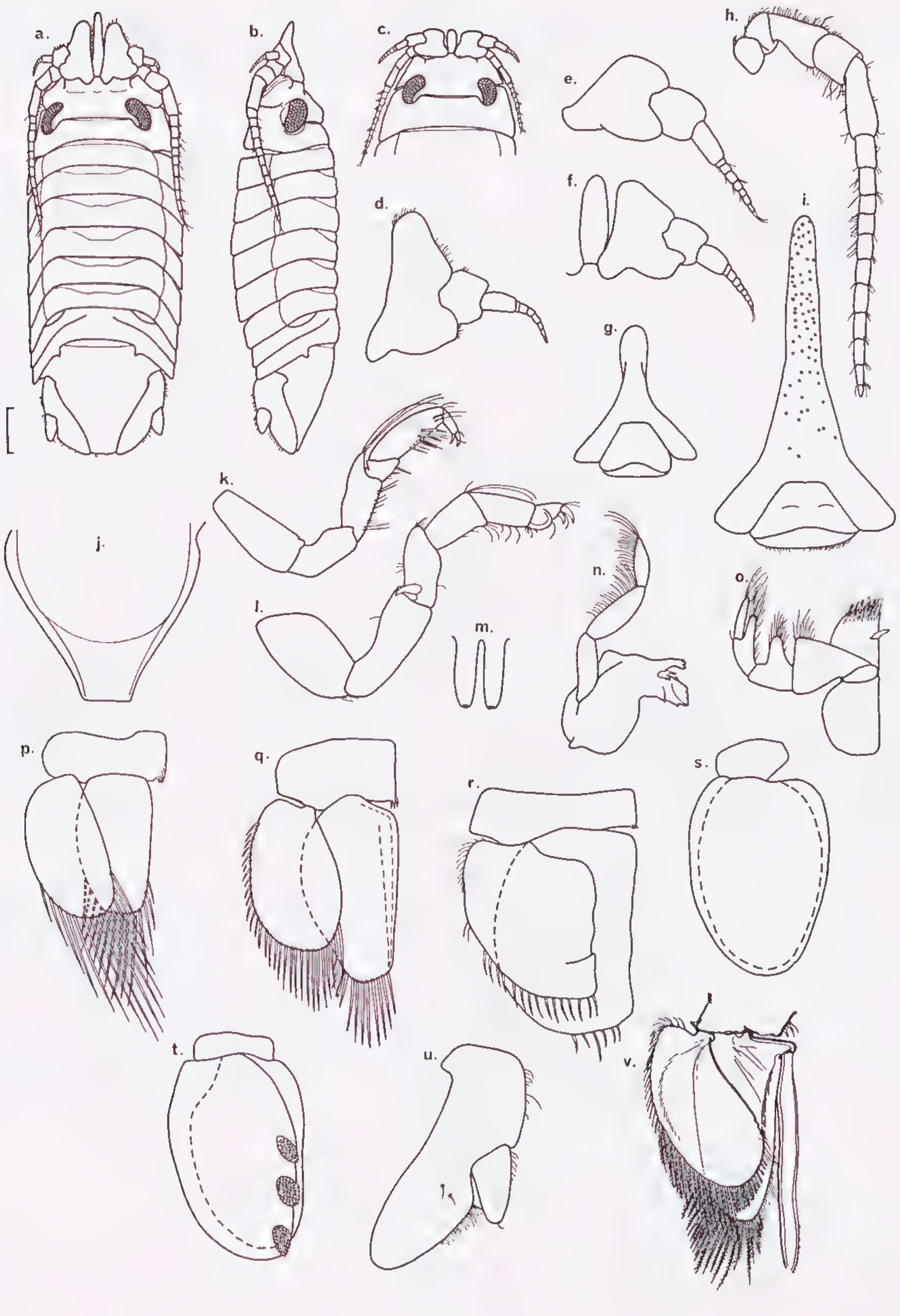

Figure 6. *Chitonopsis hanseni* Nierstrasz. Adult male (type); **(a)** dorsal; **(b)** lateral; **(d)** antennule; **(h)** antenna; **(i)** epistome and labrum — ventral; **(j)** pleotelson — ventral; **(k)** pereopod 1; **(l)** pereopod 2; **(m)** penes; **(n)** right mandible; **(o)** maxillipede; **(u)** uropod; **(v)** pleopod 2 (from Nierstrasz, 1931: Fig. 128). Ovigerous female (type) **(c)** dorsal anterior; **(e)** antennule; **(g)** epistome and labrum — ventral. Sub-adult male (type) **(f)** antennule and epistome dorsal; **(p)** to **(t)** pleopods 1 to 5 respectively (blood lacunae and setules on plumose setae omitted). Scale line represents 1 mm.

itself. Margins of appendix masculina sub-parallel, tip slightly dilated. Both rami with terminal margins of plumose setae half length of ramus bearing them. *Uropods.* Three times as long as wide; exopod sub-triangular, quarter length of endopod and housed in notch on outer margin mid-way between proximal margin and apex.

Sub-adult male. Body length 6.35 mm (Fig. 6f, p-t).

Differs from adult male in having epistome contiguous dorsally with anterior quadratic projection of cephalosome, and extending anteriorly to same level as the antennular peduncle. *Antennae.* Antennular peduncle article 1 produced anteriorly relatively less than that of adult male. *Penes.* Separate, twice as long as wide. *Pleopods.* Pleopod 1 with rami elliptical, sub-equal, with terminal margin of plumose setae sub-equal in length to the ramus bearing them. Pleopod 2 with appendix masculina not free from internal margin of endopod, but visible as a marginal thickening. Pleopod 3 with exopod slightly smaller than endopod, both rami with sparse terminal margin of short plumose setae. Pleopod 4 with both rami sub-ovate, lacking respiratory folds and setae. Exopod slightly larger than endopod. Pleopod 5 with rami sub-equal, elliptical, lacking respiratory folds and setae. Inner distal margin of exopod bearing three equidistant, finely-toothed bosses. None of the rami of any of the pleopods showing signs of articulation.

Pereopods, mouthparts, uropods and general body configuration as in adult male.

Ovigerous female. Body length 6.44 mm (Fig. 6c, e, s)

Secondary sexual dimorphism apparent, female differing from adult male in its smaller size and the form of the epistome and antennae. Antennular peduncle article 1 lacking pronounced anterior projection, extending little beyond article 2. Antennular flagellum of 7 articles. Antennal flagellum of 12 articles. Epistome contiguous with anterior quadratic projection of cephalosome and extending anteriorly to same level as antennular peduncle article 1. Further secondary sexual dimorphism lacking. Brood pouch composed of paired brood plates (specimen too damaged to allow detailed examination). Mouthparts not metamorphosed.

REMARKS: In his original description, Nierstrasz (1931: 221) stated that his Fig. 127 illustrated pereopod 5. In fact, this illustration is of pereopod 1, clearly showing the reduced carpus of that limb.

The pleopods of the adult male and ovigerous female specimens are now missing and their present whereabouts is unknown (S. Pinkster pers. comm.). It is unlikely, however, that the pleopods of the sub-adult male — excepting pleopod 2 — differ significantly from those of the adult.

### Genus **Waiteolana** Baker, 1926

*Waiteolana* Baker, 1926: 276, 277, 279, pl. 1. Nierstrasz, 1931: 222.

Type species — *W. rugosa* Baker, 1926.

GENERIC DIAGNOSIS: Body strongly sculptured, narrow, vaulted not depressed, lacking projections. Coxal plates directed ventrally, those of pereonites 2 to 7 separated from tergites by sutures. Pleonal tergite bearing three suture lines; anterior entire, posterior two absent in mid-line. Endopod of uropod not reaching as far as indented apex of sub-triangular pleotelson. Exopod half length of endopod. Antennules juxtaposed to ventral margin of cephalosome. Pereopods ambulatory, unmodified. *Adult male.* Form of penes unknown (specimen damaged). Tapering appendix masculina present, arising from proximal internal angle of endopod of pleopod 2 and extending beyond both rami.

Exopods of pleopods 3 to 5 each with sub-terminal, complete articulation. Rami of pleopod 3 with many, and of 4 with several, plumose setae. Inner margin of exopod of pleopod 5 with five finely-toothed bosses, three on distal article and two on proximal article. *Female* unknown.

### **Waiteolana rugosa** Baker, 1926

*Waiteolana rugosa* Baker, 1926; 276, 277, 279, pl. 1. Nierstrasz, 1931: 222.

PREVIOUS RECORDS: Off Wata Mooli, New South Wales, 1 male.

HOLOTYPE: Australian Museum Reg. No. G. 2275, 1 adult male and 3 microslides.

TYPE LOCALITY: Off Wata Mooli, N.S.W.

MATERIAL EXAMINED: Off Wata Mooli, N.S.W.; trawled 3.5-4 miles (5.6-6.4 km) off shore, mud, depth 54-59 fathoms (99-104 mm); 1 male (holotype); coll. E. R. Waite, 22 March 1898 ("Thetis" Expedition Station 57); Australian Museum Reg. No. G. 2275.

SPECIFIC DESCRIPTION: Adult male. Body length 7.82 mm (Fig. 7a-n).

Body deeply vaulted, two and a half times as long as broad; lateral margins sub-parallel; fine dorsal ornamentation over entire surface. Cephalosome twice as wide as long. Eyes large, strongly convex. Pereonites 1 to 7 sub-equal. Coxal plates of 1 extended anteriorly ventral to eyes. Coxal plates of 2 to 7 ventrally directed, with smoothly rounded margins; not contiguous; and separated from their tergites by obvious suture lines. Pleonal tergite showing evidence of four segments. Anterior segment as wide as tergum of pereonite 7 with entire posterior margin marked by suture line. Second segment reaching lateral margins of body and fused in mid-line to succeeding two. Pleotelson sub-triangular, apex weakly indented with a shallow groove ventrally.

*Antennae.* Antennular peduncle articles rugose, 1 and 2 expanded anteriorly, just visible in dorsal view. Flagellum of 7 articles. Antenna robust; peduncle article 5 and seven flagellar articles densely setose on external margins. *Mouthparts.* Epistome sub-triangular, flat, extended anteriorly, apex just visible in dorsal view; proximally semi-encloses sub-circular labrum. Mandible with well formed, smoothly rounded, entire incisor process; molar process narrow, acute. Maxillule missing from specimen. Maxilla with lobes slender, bearing stout terminal setae. Maxillipede with palp well produced with articles 2 to 4 bearing pronounced lobes with short terminal setae; article 5 extending beyond lobe of article 4. *Pereopods.* All ambulatory. Pereopod 1 more robust than succeeding, carpus reduced. Inferior margins of merus, carpus and propus of all pereopods bearing spines, those on 1 very stout. Dactylus of all with robust unguis and small secondary unguis. *Penes.* Unknown (holotype damaged). *Pleopods.* Endopod of pleopod 1 almost three times as long as wide, tapering to acute apex. Posterior surface bearing fine ridge next to, and parallel with, inner margin for most of length. Exopod sub-ovate, shorter than endopod. Both rami with terminal border of plumose setae. Exopod of pleopod 2 elliptical, shorter than endopod. Endopod tapering to rounded apex, proximal internal margin bearing a narrow appendix masculina longer than ramus and tapering to an acute tip. Both rami with terminal, and exopod with external, margin of plumose setae. Endopod of pleopod 3 semi-circular with inner margin straight. Exopod sub-ovate with strongly marked, complete, sub-terminal articulation. Both rami with terminal border of plumose setae. Rami of pleopod 4 sub-equal, twice as long as wide, lacking respiratory folds and having several terminal, plumose setae. Exopod with marked, complete sub-terminal articulation; external border bearing simple setae. Both rami of pleopod 5 lacking respiratory folds. Exopod twice as long as wide with

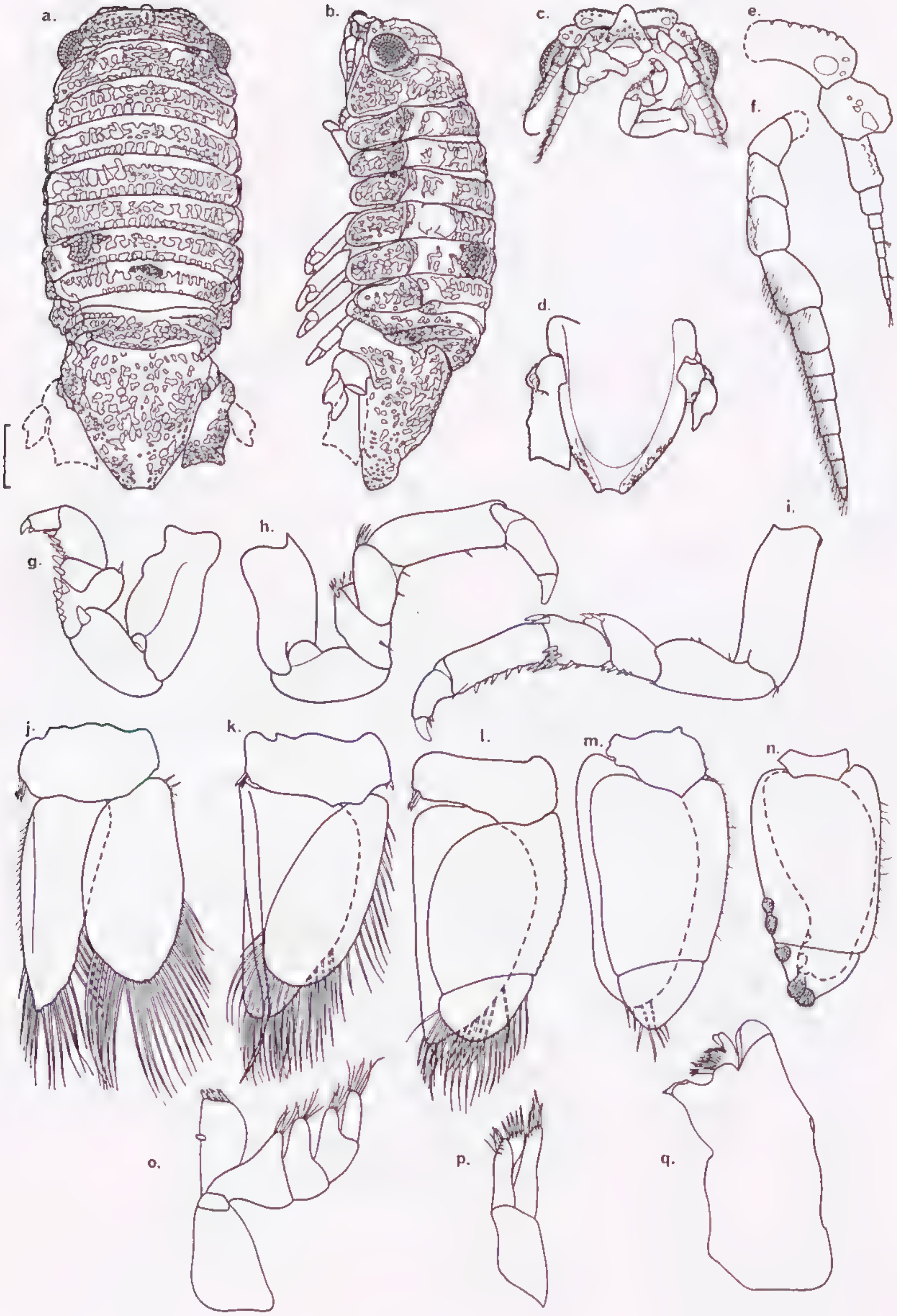

Figure 7. *Waiteolana rugosa* Baker. Adult male (holotype) **(a)** dorsal; **(b)** lateral; **(c)** ventral anterior; **(d)** pleotelson and uropods—ventral; **(e)** antennule; **(f)** antenna; **(g)** pereopod 1; **(h)** pereopod 4; **(i)** pereopod 7; **(j)** to **(n)** pleopods 1 to 5 respectively (blood lacunae and setules on plumose setae omitted); **(o)** maxillipede; **(p)** maxilla; **(q)** left mandible (palp omitted). Scale line represents 1 mm.

sub-terminal, complete articulation and simple setae on external border. Inner margin of proximal article of exopod having two finely-toothed bosses near articulation. Distal article with one such boss near articulation and two larger contiguous bosses apically. Endopod damaged on holotype. *Uropods.* Endopod not extending as far as apex of pleotelson; external border sinuous; truncate apex assymetrically emarginate. Exopod half length of endopod, free, elliptical with deep notch in distal, external margin.

### Genus **Platysphaera,** gen. nov.

Synonyms — none.

Type species — *P. membranata* sp. nov.

GENERIC DIAGNOSIS: Body flattened with a membranous extension to circumference; dorsally lacking marked ornamentation and projections. Cephalosome not reaching lateral margins of body. Antennular peduncle articles 1 and 2 expanded as flattened lobes anterior to cephalosome, not separated in mid-line by epistome. Coxal plates of pereonites 2-7 separated from tergites by sutures. Single pleonal tergite lacking sutures. Pleotelson with apex entire, lacking notch or groove. All pereonites and pleonite reaching lateral margins of body. Pereopods ambulatory, unmodified. Both rami of pleopod 3 lacking articulations; bearing long plumose setae. Exopod of pleopod 4 two-articled. Exopod of pleopod 5 with two faint, weakly-toothed bosses. Uropods not meeting in posterior mid-line; exopods reduced, situated anterior to endopods, not housed in notch. Sexual dimorphism not pronounced. *Adult male.* Penes simple, short, separate to base. Appendix masculina present, arising near interno-proximal angle of endopod of pleopod 2 and extending beyond both rami. *Ovigerous female.* Mouthparts not metamorphosed. Ventral pereonal surface as smooth, continuous cuticle, lacking obvious openings and completely enclosing brood. Pereopods 2 to 4 with short brood plates not overlapping in mid-line.

Etymology — Gr. platus + sphaera i.e. flat sphere (flattened sphaeromatid) (feminine).

### **Platysphaera membranata,** gen. nov., sp. nov.

Synonyms — none.

MATERIAL EXAMINED: Holotype male, 1.84 mm. Queensland Museum Reg. No. W.6327 (+ 1 microslide).

TYPE LOCALITY: Mellish Reef, Central Coral Sea, 17°28′S, 155°55′E. In dead coral in lagoon, depth 6 m. Coll. N. L. Bruce, 01 May 1979.

ALLOTYPE: Ovigerous female, 2.7 mm. Queensland Museum Reg. No. W. 6328. Long Island, Chesterfield Reefs, Central Coral Sea, 19°53′S, 158°28′E. Seaward edge, depth 12 m. Coll. N. L. Bruce, 05 May 1979.

ADDITIONAL PARATYPES: Coral cay, North of Long Island, Chesterfield Reefs Central Coral Sea. In pool at reef rim, depth 2 m. Coll. N. L. Bruce, 05 May 1979. 1 ovigerous female. Queensland Museum Reg. No. W.6329 (+ 2 microslides of antennae, pereopods, uropod, mouthparts).

— Long Island, Chesterfield Reef. Seaward edge of reef, depth 15 m. Coll. N. L. Bruce, 06 May, 1979. 1 immature specimen.

— Mellish Reef, Central Coral Sea. Depth 20 m. Coll. N. L. Bruce, 01 May 1979. 1 immature specimen.

Etymology — *Platysphaera* + L. membranata i.e. membraned.

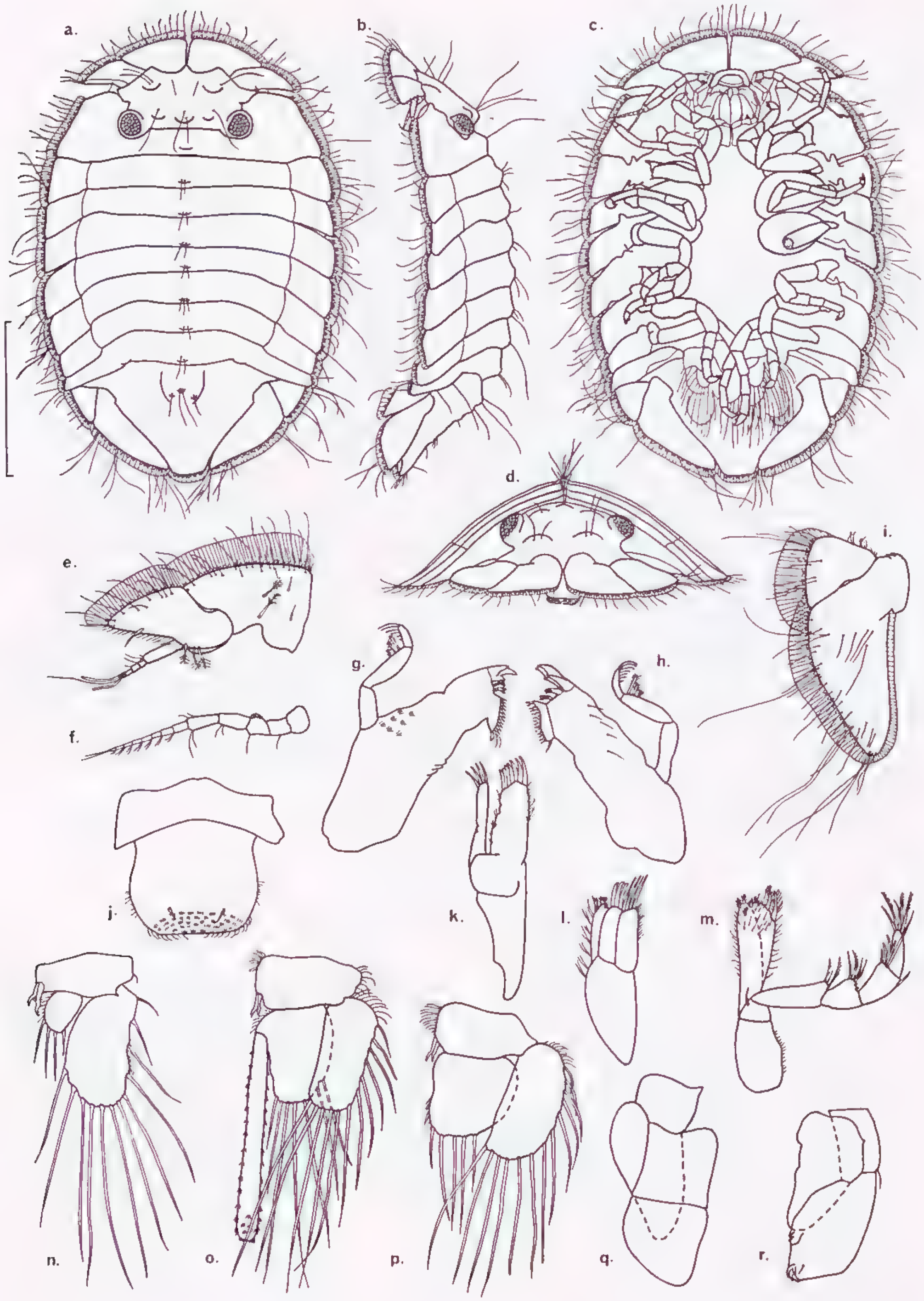

Figure 8. *Platysphaera membranata* gen. nov., sp. nov. Ovigerous female paratype (non-allotype) **(a)** dorsal; **(b)** lateral; **(c)** ventral; **(d)** anterior; **(e)** antennule; **(f)** antenna; **(g)** right mandible; **(h)** left mandible; **(i)** uropod; **(j)** epistome and labrum; **(k)** maxillule; **(l)** maxilla; **(m)** maxillipede. Adult male (holotype) **(n-r)** pleopods 1-5 respectively (setules omitted from plumose setae). Scale line represents 1 mm.

SPECIFIC DESCRIPTION: Adult male. Body length 1.84 mm. (Figs 8n-r, 9h).

Body elliptical, one and a half times as long as wide; flattened, coxal plates directed laterally. Margins of antennules, pereon, pleon, uropods and pleotelson closely applied, producing a regular, sub-continuous outline. Entire margin bearing a narrow "membrane" (apparently formed from fused setae). At junction of "membrane" with true margin, margin bearing short, separate "pegs" embedded in membrane base. Circumference of body also bearing a fringe of irregular, long setae. Cephalosome twice as wide as long with a short, acute projection in the anterior mid-line and an obtuse projection either side of this. Dorsal surface of cephalosome with 5 tubercles; two anterior — at bases of obtuse anterior projections — and three in a transverse row between the eyes. Eyes sub-circular, darkly pigmented, very convex, occupying the postero-lateral angles of the cephalosome. Pereonite 1 extending anteriorly lateral to the eyes, juxtaposed to article 2 of antennule. Pereonites 2 to 7 and pleonite sub-equal, each having a slight setose tubercle in dorsal mid-line, additional ornamentation absent. Pleotelson domed, sub-triangular, apex broadly truncated; anterior mid-line bearing a raised boss, additional ornamentation absent.

*Antennae.* Antennular peduncle articles 1 and 2 strongly flattened, article 1 twice length of article 2. Article 3 unmodified, five times as long as broad, sub-equal in length to article 2. Flagellum of four articles, distal two each bearing one aesthetasc. Antennules juxtaposed in animal's mid-line, not separated by epistome. Antennal articles not expanded. Peduncle articles sub-equal in length; article 1 sub-circular, article 3 with superior lobe bearing several "scales". Flagellum of nine articles. Antenna sub-equal in length to antennule. *Mouthparts.* Epistome transverse anteriorly, not extended between antennules or beyond cephalosome; not embracing labrum proximally. Mandibles slender, incisor processes and palps well developed, molar processes short, oblique, serrate. Left mandible with incisor process of four stout teeth. Lacinia mobilis as a notched peg, and a short setal row. Right mandible with incisor process of three stout teeth, and a setal row. Second article of each palp with three plumose setae on infero-distal margin. Maxillule with seven simple spines on exopod and four pectinate spines on endopod. Maxilla with four long, simple spines on each of outer two lobes and shorter plumose spines on inner lobe. Maxillipede with endite narrow, four times as long as broad, lacking coupling hooks; distal margin bearing two long, external, and a group of short, internal plumose setae. Palp slender, articles 2 to 4 bearing low, inferior lobes; articles 2 to 5 bearing short, weakly-plumose setae. *Pereopods.* Pereopod 1 more robust than succeeding pereopods; carpus reduced; propus with three antero-distal, plumose setae. Pereopods 2 and 3 sub-equal, slender; ischium, merus, carpus and propus sub-equal in length. Pereopod 4 slightly more robust than 3, carpus reduced. Pereopods 5 and 6 sub-equal, slightly more robust than pereopod 4 with carpi slightly longer. Pereopod 7 longer than, and more slender than, pereopod 6; carpus not reduced, with postero-distal margin bearing five stout plumose setae not found on other pereopods. *Penes* simple, separate to base; each twice as long as wide with smoothly rounded tip. *Pleopods.* Interno-distal angle of basis of pleopod 1 with two coupling hooks. Rami sub-elliptical, markedly unequal; exopod five times the size of the endopod, with one simple externo-proximal seta, three external plumose setae and a terminal margin of plumose setae one and a half times the length of the ramus. Endopod with four short, terminal setae. Basis of pleopod 2 bearing two coupling hooks. Exopod sub-rectangular, equal in length to sub-ovate endopod. Endopod bearing an appendix masculina originating near interno-proximal angle and being separated from the ramus by an articulation. Appendix masculina flat, twice as long as ramus with sub-parallel sides bearing microtrichia and a rounded, truncated apex bearing several non-marginal microtrichia. Both rami with terminal, plumose setae twice length of rami, and exopod with external margin of setae. Basis of pleopod 4 lacking coupling hooks. Exopod sub-rectangular, one and a half times the length of narrowly sub-ovate endopod. Both rami lacking setae and respiratory folds. Exopod bearing transverse articulation mid-way along length, separating sub-quadratic, proximal article from sub-quadrantic distal article. Endopod lacking articulations. Basis of pleopod 5 lacking coupling hooks. Rami sub-equal in length but exopod extending beyond endopod. Endopod narrowly sub-ovate, exopod sub-elliptical; both rami lacking setae, folds and articulations. Exopod with two very weakly toothed bosses on internal margin, one apical and one sub-apical. *Uropods*. Each with endopod broad, four times the size of exopod, sub-triangular, juxtaposed to lateral margin of pleotelson and not extending beyond level of its apex. Exopod sub-triangular, arising from anterior-proximal margin of endopod and occupying region between endopod and pleonite.

Ovigerous female. Body length 2.7 mm (figs 8a-m, 9a-g).

Differs from the above description of the male only in primary sexual characters and — in the specimens examined — by its larger size. Brood enclosed by ventral cuticle, which is smooth and apparently devoid of openings. Pereopods 2 to 4 with short brood plates not overlapping in mid-line. Brood number 6 to 8 (approximately 6 late stage embryos in allotype, 8 ova in second ovigerous female paratype). Mouthparts unmodified.

REMARKS: The type series contained only one adult male specimen, which has been designated the holotype. Due to the undesirability of dissecting the holotype, only the pleopods from one side have been removed for figuring (fig. 8n-r). The remaining figures are of an ovigerous female paratype (non-allotype) and while the written description of the male is based — for fine detail — on the appendages of this female (the use of immature specimens being considered unsatisfactory for this purpose), the holotype has, as far as possible, been compared closely to the female and any differences have been incorporated in the holotype's description.

In the ovigerous female it proved impossible to tell whether the ventral cuticle is composed of the sternites (with the brood housed within the body e.g. in the oviducts), or fused folds of cuticle (with the brood in a pouch ventral to the sternites). More specimens are needed to decide this, but it is more probable that the latter is the case as ventral 'pockets' of cuticle are found in platybranch genera closely related to *Platysphaera* (e.g. *Leptosphaeroma* sp.: Hansen, 1905: 79, 80; *Syncassidina* — see above).

Of the known sphaeromatid genera, *Platysphaera* appears to be most closely related to *Leptosphaeroma* Hilgendorf, especially with regard to the cephalosome and pereon. The mandibles show a similar form and pereopod 1 is more robust than the other pereopods in both genera. *Platysphaera* differs from *Leptosphaeroma* in the form of the pleon and pleotelson. In *Leptosphaeroma* the pleonal tergite is divided by two sutures reaching the lateral margins, and the endopods of the uropods meet in the mid-line beyond the pleotelsonic apex. The uropodal exopods of *Leptosphaeroma* are housed in lateral notches, the anterior margins of these notches being reduced to narrow spines (Nishimura, 1976). In *Platysphaera* this region of uropod appears to have been lost completely, leading to the condition of the exopod lying anterior to the endopod.

The pereopods of *Platysphaera* are unusual in that pereopod 4 has a reduced carpus similar to that of pereopod 1. Pereopods 5 and 6 show a similar, though less pronounced, reduction.

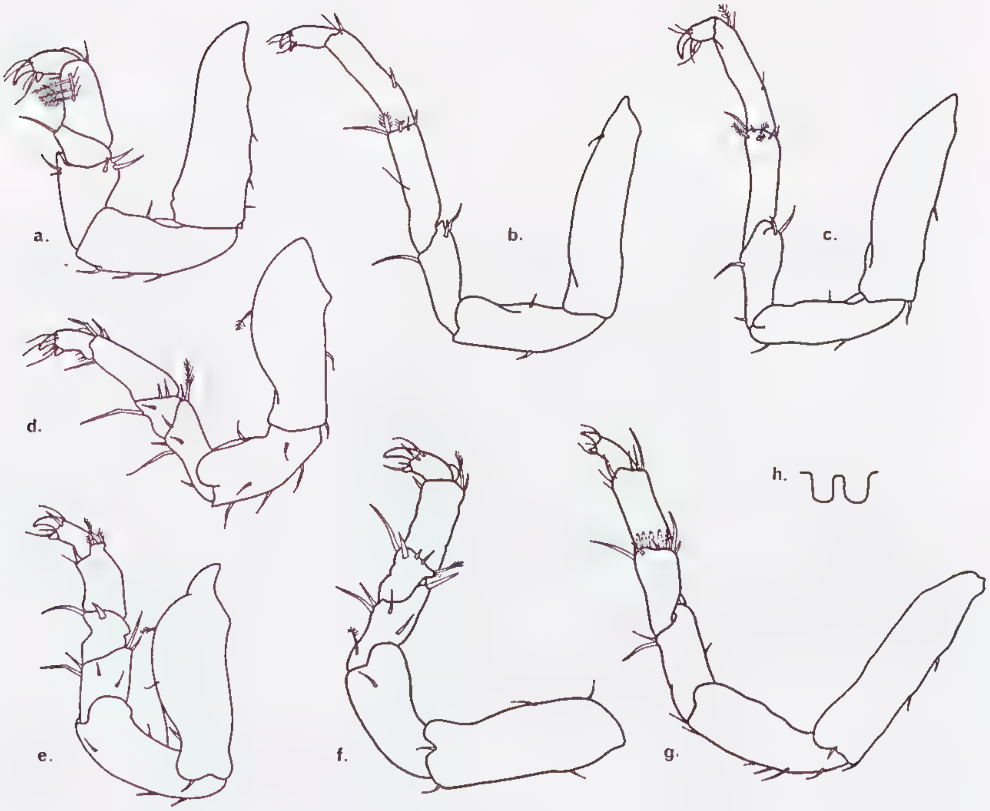

Figure 9. *Platysphaera membranata* gen. nov., sp. nov. Ovigerous female (non-allotype) **(a-g)** pereopods 1-7 respectively. Adult male (holotype) **(h)** penes.

It is noteworthy that many new platybranch species are proving to be members of new genera, showing the Platybranchiatinae to be a very diverse group. It is to be expected that many new species and genera remain to be discovered, and these will hopefully provide much information that will aid our understanding of the Sphaeromatidae as a family.

## ACKNOWLEDGEMENTS

Thanks are due to the Nuffield Foundation and the Natural Environment Research Council for research grants which made this work possible, and to: P. Arnold (James Cook University); R. W. George (Western Australian Museum); A. Green (Tasmanian Museum); J. K. Lowry (Australian Museum); R. Monroe (Queensland Museum); S. Pinkster (Zoological Museum, Amsterdam); G. C. B. Poore (Victorian Fisheries and Wildlife Division); W. Stephenson and S. D. Cook (University of Queensland); T. Wolff (Zoology Museum, University of Copenhagen) and W. Zeidler (South Australian Museum) for the loan or gift of material. Special additional thanks are due to Peter Arnold for providing much ecological and other relevant information about *P. pectinata* and to N. L. Bruce (Queensland University) for donating the material on which the new genus was founded. A. H. Sommerstein (Dept. of Classics, Nottingham University) kindly checked the construction of the new names.

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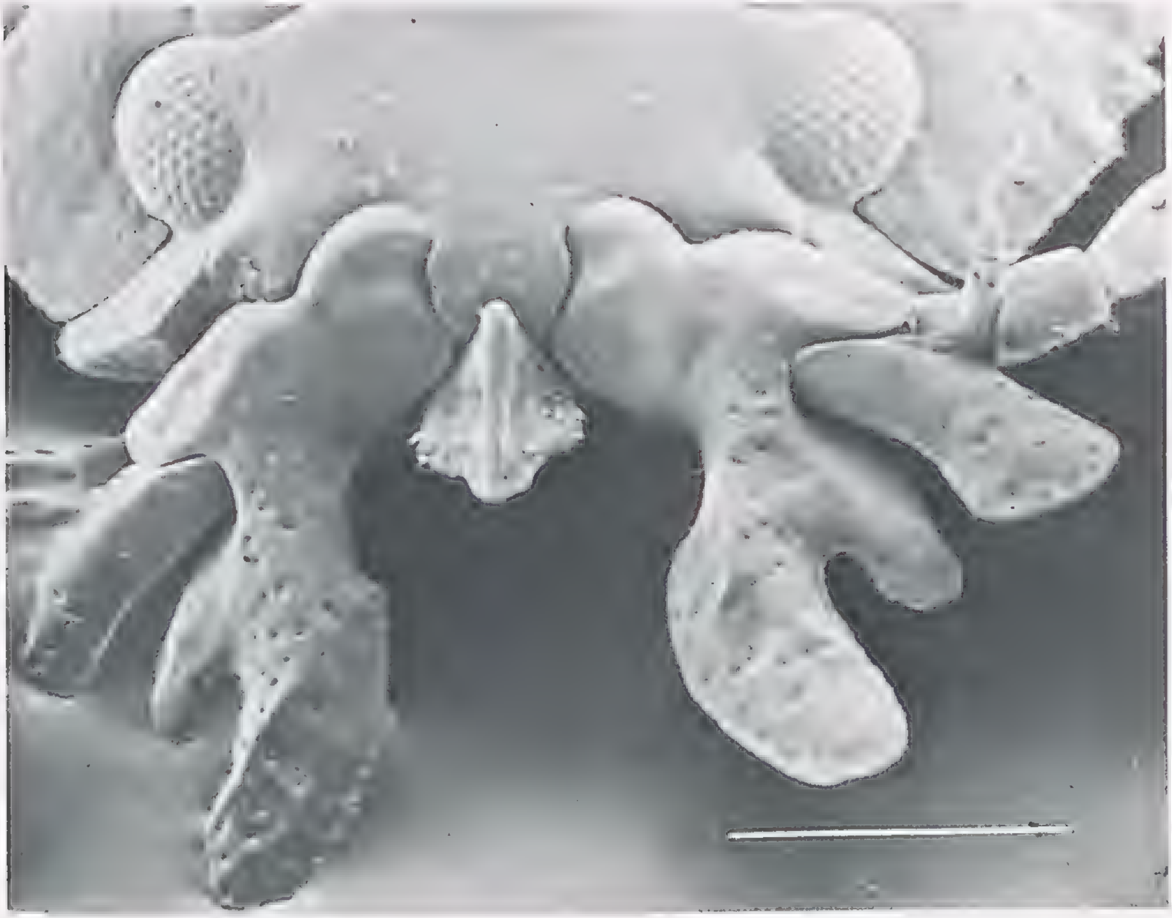

Figure 10. Scanning electron micrograph of the cephalosome of a male *Paracassidina pectinata* Baker from Queensland. (Coated in gold with a polaron Sputter Coater and viewed with a Cambridge 600 SEM). Scale bar equals 0.5 mm.

# THE CIROLANIDAE (CRUSTACEA: ISOPODA) OF AUSTRALIA: NEW SPECIES AND A NEW GENUS FROM SOUTHEASTERN AUSTRALIA

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## SUMMARY

New species of the isopod family Cirolanidae are described and figured. These include *Eurydice acuticauda, E. spenceri, Cirolana bathynella, C. halei, C. triloba, C. furcata, C. similis, C. victoriae* and a new genus and species *Orphelana perplexa*. Their systematic position within the respective genera is discussed. All species except *C. victoriae* and *E. spenceri* are known to be from subtidal habitats.

## INTRODUCTION

Since the work of Hale (1925; 1940) there has not been a single publication dealing specifically with Australian cirolanid isopods. Naylor (1966) listed three species for Port Phillip Bay and Nordenstam (1946) recorded a further species from Cape Jaubert. This present work is the third in a series that deals exclusively with the family Cirolanidae from Australian seas. The first (Bruce, 1980), dealt with a collection from the Great Barrier Reef, whilst the second dealt with a single genus of sand beach cirolanids from Queensland Bruce, *in press*).

The new species described were obtained from the following collections. The Australian Museum Shelf Benthic Survey (SBS), off Sydney, NSW, Australian Museum Hunter District Water Board Survey (HDWBS), the Crib Point Benthic Survey (CPBS), the Western Port Bay Environmental Survey (WBES), and the Port Phillip Bay Environmental Study (PPBES). The collections made from the last three surveys are housed in the National Museum of Victoria. Details of the times and methods used in these collections can be obtained from Poore, *et al* (1975). Additional material was obtained from the South Australian Museum (SAM), and the Stockholm Museum of Natural History (SM(NH)). All of the collections from which these new species were taken contain other named species, which will be dealt with in future publications.

Type material has been deposited at the Australian Museum, Sydney (AM), the National Museum of Victoria, Melbourne (NMV), the South Australian Museum, Adelaide (SAM), Queensland Museum (QM) and the Swedish Museum (SM(NH)).

Records of The Australian Museum, 1981, **Volume 33 No. 13,** 644-672, Figures 1-15.

## FAMILY CIROLANIDAE

### Genus **Eurydice** Leach

### **Eurydice acuticauda** sp.nov. (Figs. 1, 2)

MATERIAL: Western Port Bay, Vic., WBES stns: 1726 (1 specimen), 1727 (1), 1733(1), 1739(4), 1743(2), 1746(1); Western Port Bay, Crib Point, CPBS stns: A2(1), C6(2), 24N(5), 25N(6), 300(1), 31S(1), 31E(1), 31N(1), 32E(1), 32S(2), 400(2), 41N(1); Port Phillip Bay, Vic., PPBES stns: 945(3), 968(3), 974(2), 986(4). NSW Shelf, Hunter District, HDWBS stns: off Belmont Beach 33°02′36″S, 151°40′56″E, 19m, 20.5.1975, (1 specimen) and 20 m, 20.9.1975, (1); off Burwood Beach, 32°57′31″S, 151°44′43″E, 22 m, 31.10.1975, (1) and 20 m, 28.1.1976, (2); off McMasters Beach, Gosford, 33°30′S, 151°125′E, 20 m, 22.11.1975 (1).

TYPES: Holotype ♂, NMV Reg. No. J654
Paratypes 2♂ and 6♀♀ NMV Reg. No. J655-659.
Paratypes AM Reg. No. P23053 — 23056, P23156
Paratypes SAM Reg. No. C3865
Paratypes QM Reg. No. W8036

TYPE LOCALITY: Western Port Bay, Victoria, WBES stn. 1739, 26.11.73. Paratypes from NSW, and Western Port Bay.

DESCRIPTION OF MALE: Mouthparts as for the genus. Body elongate, straight sided. Eyes moderately large, red or black.

Antennule with all articles (Fig. 1 (h)) short, approximately sub-equal in length; flagellum short composed of three articles, proximal article as long as peduncle, provided with numerous aesthetascs. Antenna (Fig. 1(g)) long, peduncle extending to middle of pereonite 1; peduncular article 3 as long as combined length of articles 1 and 2 and about half as long as article 4; flagellum extremely long, extending to or just beyond apex of telson, flagellar articles elongate, each with plicate process (Fig. 2(b)) at distal end.

Coxae with posterior margins only slightly produced (Fig. 1(a)), those of pereonites 5-7 with or without slight points.

Pereopod 1 (Fig. 1(f)) short, with few setae; prominent spine present on anterior distal angle of ischium; posterior borders of merus, carpus and propodus with 4, 1 and 3 spines respectively, distal spine of the propodus opposes dactyl (Fig. 1(e)) which has a well developed secondary unguis. Pereopods 2 and 3 similar to pereopod 1 but less robust. Pereopod 7 (Fig. 1(d)) large, anterior margin of all articles except basis with numerous setae, ischium with 2 prominent spines on anterior distal angle, merus with 2 groups of spines on the margins, and a further group on each distal angle, as has the carpus; propodus with two single spines and single terminal spine. Posterior margins with fewer setae, each article except basis with two groups of spines and a third group at the distal angle. Pereopod 6 similar to pereopod 7, but slightly longer, pereopods 4 and 5 shorter.

Pleonite 1 largely concealed. Pleopods as for the genus, appendix masculina (Fig. 2(c), (d), (e)) extending beyond inner ramus by 0.2 of its length, slightly recurved, apex coming to a blunt point.

Telson about as long as broad, posterior margin (Fig. 2(a)) forming an acute angle, provided with 12 plumose setae, each set within a notch. Uropods (Fig. 1(c)) not extending beyond posterior margin of telson, peduncle armed with row of about 12 stout

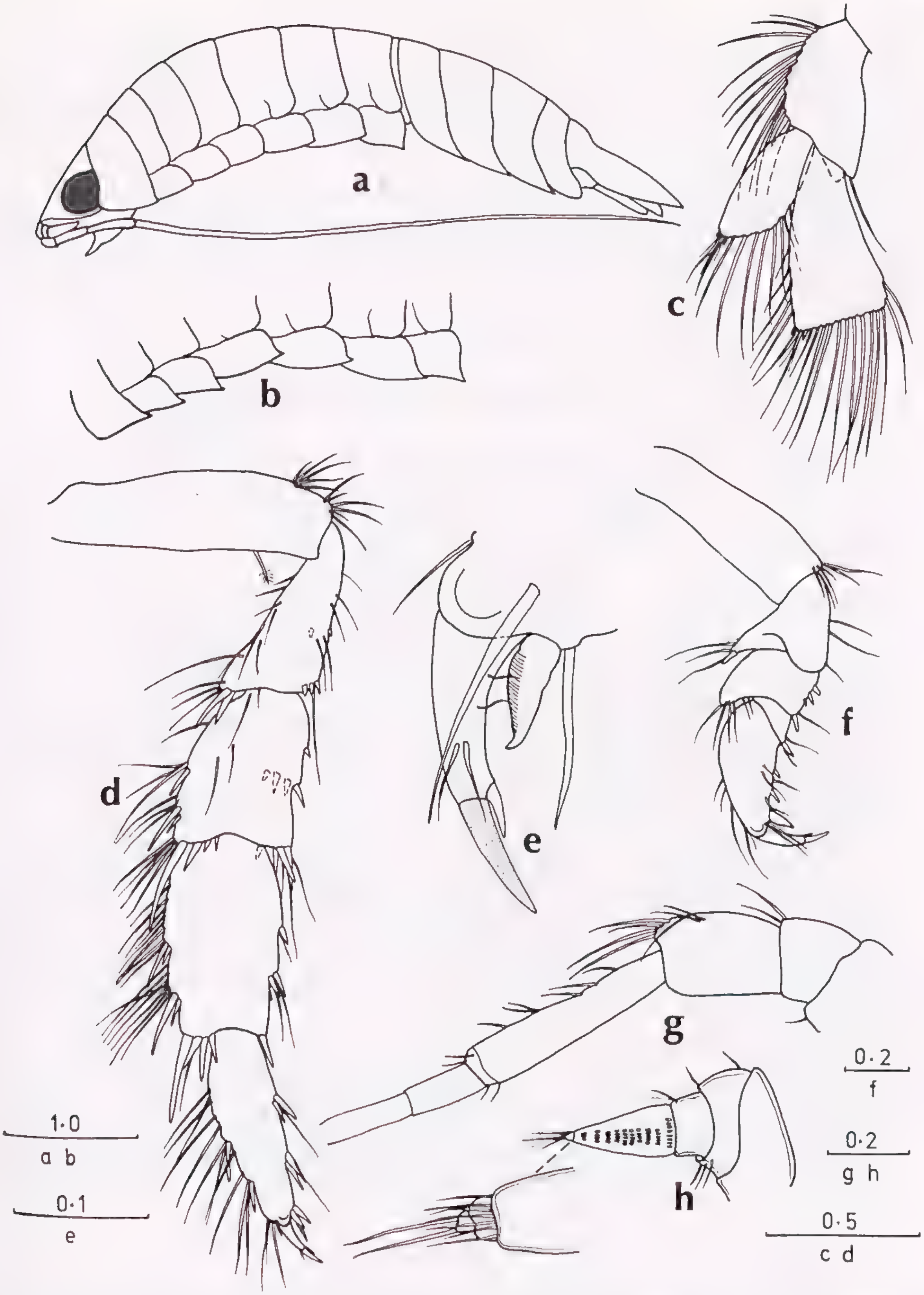

Figure 1. *Eurydice acuticauda* sp. nov. **(a)** lateral view, holotype **(b)** coxae of ♀, PPB **(c)**-**(h)** ♂ paratype **(c)** uropod **(d)** pereopod 7 **(e)** dactyl of pereopod 1 **(f)** pereopod 1 **(g)** antennal peduncle **(h)** antennule. Scale line, mm.

setae and a single spine; exopod sub-ovate, about half as long as endopod, posterior margin with 8 long plumose setae, outer distal angle with two small spines and a group of about 6 setae; outer margin with 3 small setae. Endopod with posterior margin truncate, armed with about 13 plumose setae; lateral margin with 5 plumose setae; outer distal angle with 2 small spines between which lie a group of simple setae.

FEMALE: The female has a shorter pleon, and more ovate vaulted body shape. The coxae of the pereonites are with or without acute points on the postolateral margins (Fig. 1(b)). The antennae are slightly shorter, and lack the plicate process. Otherwise, the female differs only in lacking the sexual characters.

SIZE: Largest female 6.5 mm, largest male 5.5 mm.

COLOUR: Reddish brown with black chromatophores in alcohol.

REMARKS: This species can be readily separated from all other species by the telson which is totally lacking in spines and forms a point, the only other species in which this occurs is *E. humilis* Stebbing, 1910, which possesses a very narrow hind margin. The appendix masculina, the well developed secondry unguis of pereopod 1 and the short uropodal exopod also serve to distinguish this species.

Variation. This species shows a certain degree of variability, both sexual and geographical. The presence or absence of points on the coxae has long been considered an important character in the taxonomy of *Eurydice* species. That these are poorly developed in the males, while the females possess them is a variation not previously noted for the genus. Furthermore there is variation in the degree of development of these coxal points, some being conspicuous, others less so. This variation in coxal point development is not correlated to locality, nor to size. Only in the New South Wales material do they appear constant. It is also unusual that eye colour varies, though this apparently does occur in other species of Cirolanidae.

More striking differences are present in the specimens from Port Phillip Bay, though these differences are largely confined to the males. The antennae of Port Phillip Bay males lack the plicate process and both sexes have shorter flagellar articles (Fig. 2(g)) than that of the type material (Fig. 2(f)). The appendix masculina is blunt (Fig. 2(d)) rather than pointed (Fig. 2(c)), but is not shorter than that of type specimen. Also, the relative length of the penes vary, those of the type being almost twice as long as the Port Phillip Bay material of similar size.

Recent work on species of *Eurydice* (Bowman, 1977; Bruce, 1980; Bruce & Jones, 1978) and on *Excirolana chiltoni* (Richardson, 1905) (Bruce & Jones, *in press*) suggests that over a geographical area variation in morphology of various characters, including the appendix masculina is acceptable within a single species. The differences in form shown by *E. acuticauda* sp. nov. are primarily ones of degree, rather than of form, and at present the author considers best to treat them as one species, at least until the distribution of the variations shown is better known.

ETYMOLOGY: The specific name is derived from the combination of the latin words *cauda* (= tail) and *acutus* (= sharp).

DISTRIBUTION: Port Phillip Bay, Victoria from 3 to 15 m, in fine sand, and sand shell grit bottom; Western Port Victoria, and off Burwood and Belmont Beaches, Hunter River district and off McMasters Beach, Gosford, N.S.W., between 18 m and 22 m, in fine sand.

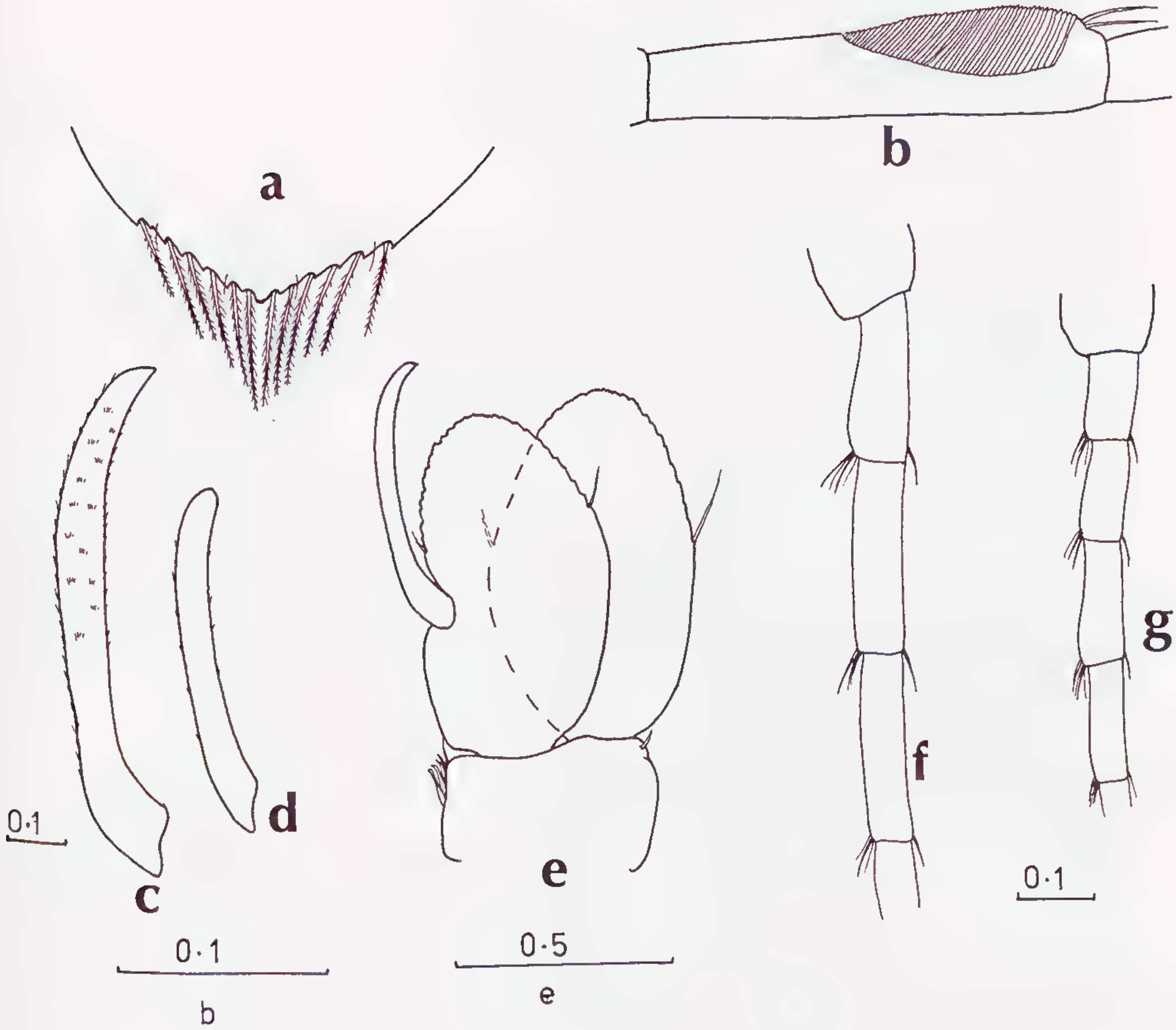

Figure 2. *Eurydice acuticauda* sp. nov. All figs from paratypes. **(a)** apex of telson **(b)** flagellar article of antenna,♂**(c)** appendix masculina, PPB. **(d)** appendix masculina, WP **(e)**♂pleopod 2, PPB, flagellar articles of antenna, **(f)** ♀ PPB **(g)** ♀ WP. Scale line, mm.

### **Eurydice spenceri** sp. nov. (Fig. 3)

MATERIAL: Label data: No. 22, Spencer Gulf, Syd. Australian. 1856. SM(NH) Reg. No. Isopodo 5718. (2♂, 9♀).

TYPES: Holotype ♂, SM(NH)) Reg. No. 3168
Paratypes 8♀♀, SM(NH)) Reg. No. 5718
Paratypes 1♂, 1♀, SAM Reg. No. C3866

TYPE LOCALITY: Spencer Gulf, South Australia, 1856.

DESCRIPTION OF MALE: Body elongate, straight sided. Eyes black. Mouthparts not differing significantly from others of the genus.

Antennule (Fig. 3(h) ) with all peduncular articles short, approximately sub-equal in length; flagellum composed of three articles, proximal article as long as peduncle. Antenna (Fig. 3(i) ) with peduncular article 3 about 0.66 as long as article 4 and twice length of article 2; flagellum extending to pleon, articles without plicate process.

Coxae 5-7 with posterior margins produced to form small point. Pleonite 1 largely concealed by pereonite 7. Paired penes present on posterior surface of sternite 7.

Pereopod 1 (Fig. 3(d) ) short, with a few setae. Anterior distal angles of ischium and merus with 2 and 4 setae respectively; posterior borders with few setae on ischium and 5 spines on merus; propodus bears 4 spines on posterior margin, terminal spine opposing dactyl (Fig. 3(e) ), anterior margin with two setae. Pereopods 2 and 3 similar to pereopod 1, but more slender. Pereopod 7 (Fig. 3(c) ) with ischium, carpus and propodus sub-equal in length, merus slightly shorter. Margins of merus, carpus and propodus with numerous spines, arranged in groups and amongst which are scattered numerous setae. Pereopod 6 similar to 7, but slightly longer.

Pleopods as for the genus. Pleopod 2 with appendix masculina (Fig. 3(g) ) extending beyond inner ramus by 0.25 of its length, distal portion spatulate in shape.

Telson slightly longer than broad, posterior margin with 16 plumose setae symetrically placed about prominent median tooth; lateral teeth also prominent; anterior dorsal surface with distinct depression. Uropods (Fig. 3(f) ) not reaching posterior margin of telson; peduncle with 14 plumose along external margin; exopod slender, ovate, about 0.3 as long as endopod which has distinctly truncate posterior margin. Distal margin of endopod with 10 plumose setae, external margin with 3; exterior distal angle with 2 small spines between which lie a group of simple setae.

FEMALE: Pleon tends to be shorter, and body shape more ovate. The antennal flagellum is shorter. Otherwise, the female closely resembles the male.

SIZE: Largest male, 6.5 mm, smallest, 5.0 mm; largest female 8.0 mm, smallest 6.0 mm.

COLOUR: Pale cream in alcohol, with an almost total absence of chromatophores, probably due to bleaching of the long preserved specimens.

REMARKS: This species, in common with the two other members of the genus known from Australia *E. orientalis* Hansen, 1890, and *E. acuticauda* sp. nov., lacks spines on the hind margin of the telson. It can be separated from *E. acuticauda* by the more excavate hind margin of the telson and the spatulate appendix masculina. Other differences include the greater number of spines on the posterior pereopods and the lack of a prominent spine on the anterior angle of the merus of pereopod 1. *Eurydice*

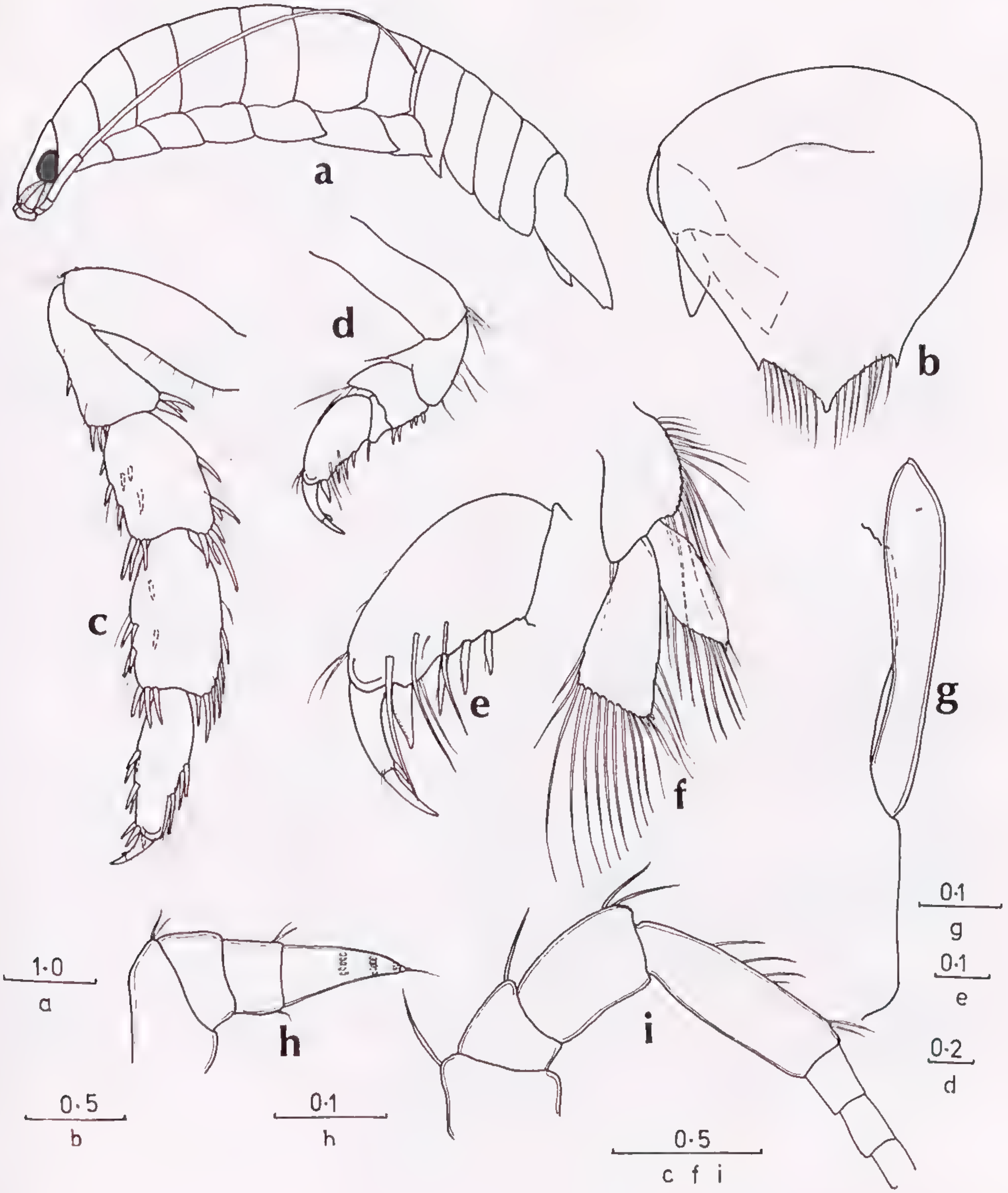

Figure 3. *Eurydice spenceri* sp. nov. **(a)** holotype, lateral view **(b)**-**(i)**♂paratype **(b)** telson **(c)** pereopod 7 **(d)** pereopod 1 **(e)** propodus, pereopod 1 **(f)** uropod **(g)** appendix masculina **(h)** antennule **(i)** antennal peduncle. Scale line, mm.

*orientalis* is readily distinguished by the truncate posterior margin of the telson.

ETYMOLOGY: The specific epithet is taken from the type locality, Spencer Gulf.

DISTRIBUTION: Known only from the type locality, from where it was taken in 1856.

## **Orphelana** gen. nov.

DIAGNOSIS: Cirolanidae with antennule peduncle 3-articulate, antennal peduncle 5-articulate, all articles short. Frontal lamina triangular, nearly obsolete. Maxilliped palp with lateral margins smoothly curved, with only a few small setae, endite with single coupling hook and terminal spine. Mandible with cutting edge narrow, obscurely tridentate, spine row with cuspidate spines; mandibular palp short, not reaching cutting edge. Maxillule with anterior distal spines of gnathal surface forming a distinct cluster set apart from the remainder, inner lobe with 3 plumose spines. Pereopods 5-7 natatory, with numerous setae. Uropod with inner margin of peduncle produced. Pleopod 1 with peduncle as long as broad, endopod shorter than exopod and 0.3 as wide, distal margin only setose, pleopod 2 with appendix masculina arising 0.3 along the inner margin of endopod; exopods of pleopods 3-5 with complete suture; endopod of pleopod 5 only glabrous. Pleonites with epimera all free, not overlapped.

RELATIONSHIPS: The mouthparts clearly distinguish this genus from others in the family. No other genus shows a similar arrangement of spines on the gnathal surface of the maxillule endite in combination with an irregular cutting edge to the mandible and a short mandibular palp. The form of the antennae, antennules and pleopods show a close similarity to those of the genus *Conilorpheus* Stebbing, 1905. Only the first and second pleopods have been figured for this genus and these correspond closely to those of *Orphelana* gen. nov. The pereopods of the genera are dissimilar as those of *Conilorpheus* are all ambulatory while the posterior pereopods of *Orphelana* are natatory.

The genus *Eurydice* also shows some similarity to *Orphelana*. The form of the pleopods are similar with elongate protopods, the appendix masculina not arising basally on the inner ramus of pleopod 2, and the exopods of pleopod 3-5 each with a distinct suture. Pereopods 5-7 are natatory, flattened and provided with numerous setae, as are the posterior pereopods of most species of *Eurydice*. *Orphelana* is readily separated from the genus *Eurydice* by the form of the uropods, in having a sessile clypeus, the antennal peduncle 5-segmented, and by differences in mouthpart morphology.

At present no discussion is offered on the absence of maxillae. These could not be located prior to dissection of the mouthparts, nor during dissection, and appears to be genuinely absent. However, whether this would be true for all specimens has yet to be confirmed.

ETYMOLOGY: The name is derived from *Orpheus*, the lover of *Eurydice* in Greek mythology, and the ending *-lana*. Gender is feminine.

## **Orphelana perplexa** sp. nov. (Figs 4-6)

MATERIAL: Holotype, 11 mm, NMV Reg. No. J660.

TYPE LOCALITY: Crib Point, Western Port, Victoria. CPBS Stn. 300, 15 m. 24.8.1967.

DESCRIPTION OF MALE: Body little more than 2.5 times as long as broad; integument thin, each segment with one or two transverse impressed lines (Fig. 4(a) ). Cephalon (Fig. 4(b) ) about twice as wide as long, deeply immersed in first pereonite, eyes absent. Frontal lamina (Fig. 4(c) ) small and triangular, clypeus sessile, lateral margins backwardly directed.

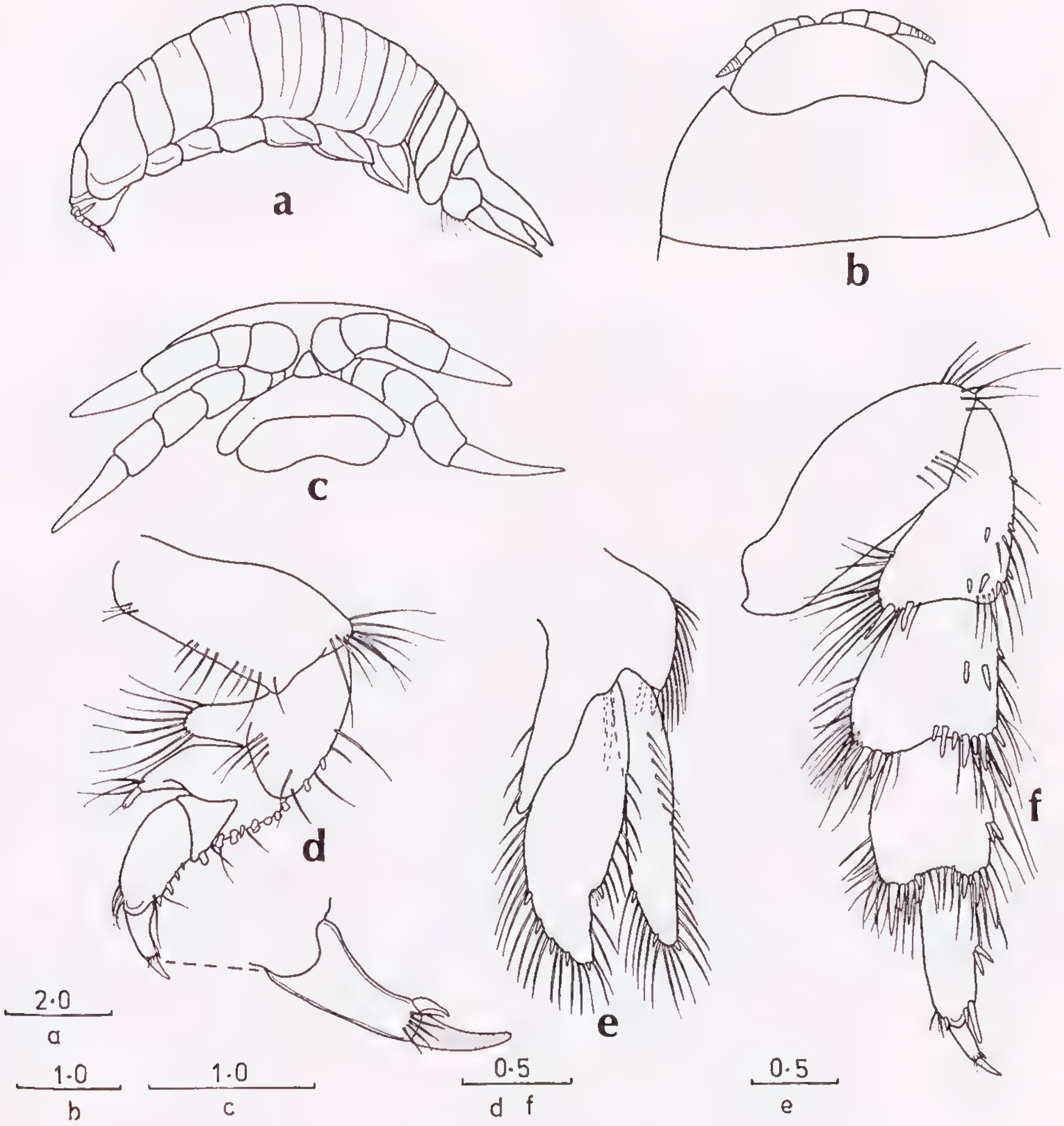

Figure 4. *Orphelana perplexa* sp. nov. Holotype **(a)** lateral view **(b)** dorsal view of cephalon and pereonite 1 **(c)** ventral view of clypeal region **(d)** pereopod 1 **(e)** uropod **(f)** pereopod 7. Scale line, mm.

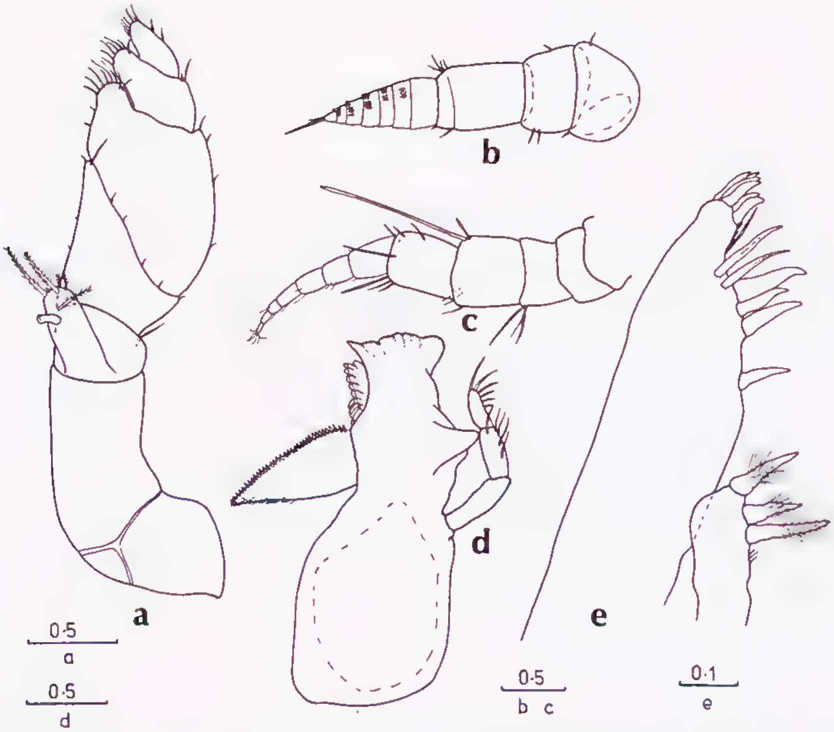

Figure 5. *Orphelana perplexa* sp. nov. Holotype **(a)** maxilliped **(b)** antennule **(c)** antenna **(d)** mandible **(e)** maxillule. Scale line, mm.

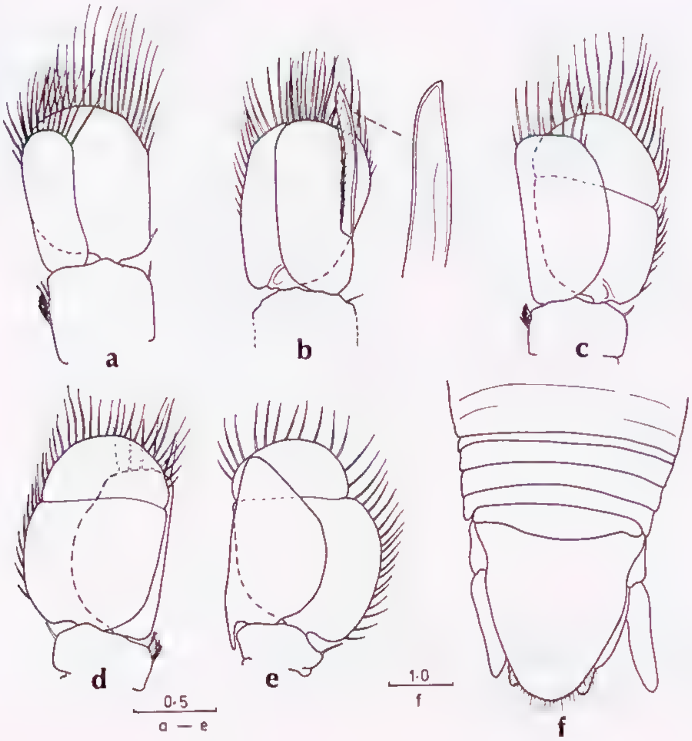

Figure 6. *Orphelana perplexa* sp. nov. Holotype **(a)**-**(e)** pleopods 1-5 respectively **(f)** pleon and telson. Scale line, mm.

Pereonite 1 little more than twice as long as pereonite 2, pereonites 5 and 6 longest. Coxae 2 and 3 (Fig. 4(a) ) with feeble longitudinal carina, coxae 5-7 with oblique carina, only moderately produced. Pleonites 1-5 visible, epimera 2-5 not overlapped, lateral margin of pleonite 4 expanded.

Antennule (Fig. 5(b) ) short, peduncular article 3 as long as combined lengths of articles 1 and 2; flagellum short, not reaching pereonite 1 (Fig. 4(a), (b) ), composed of 7 articles all but first and last with aesthetascs. Antenna (Fig. 5(c) ) with all peduncular articles short, articles 1-3 sub-equal in length as are articles 4 and 5, which are each about twice as long as peduncular article 3; article 4 with prominent long spine on the anterior distal angle. Flagellum short, consisting of 7 articles, which become progressively shorter distally.

Mouthparts. Mandible (Fig. 5(d) ) with narrow cutting edge, spine row with about 14 blunt cusp-like spines; molar about twice as long as greatest width tapering distally, armed with about 36 teeth; palp short, article 1 slightly longer than article 2 which has 5 setae on lateral margin as has article 3. Maxillule (Fig. 5(e) ) elongate with about 14 spines on gnathal surface, the distal 7 being closely grouped and set apart from the remainder. Maxilla apparently absent. Maxilliped (Fig. 5(a) ) with very few setae, lateral margins not produced, inner margins of palp segments 3 and 4 slightly produced, with few setae. Endite with single coupling hook apical spine, 3 long and 2 short plumose setae.

Pereopod 1 (Fig. 4(d) ) short, robust, basis with row of setae anterior margin and a group of setae on posterior distal angle; ischium with anterior margin produced with about 8 setae, posterior margin with 2 spines and 3 setae; merus with anterior margin produced, bearing a conspicuous spine at apex, 5 blunt spines on posterior margin; carpus short, posterior margin with single spine; propodus with 4 spines on posterior margin, dactyl with well developed slender secondary unguis. Pereopod 7 (Fig. 4(f) ) broad and flat, anterior margin of merus and carpus provided with numerous setae; inner margin with fewer setae but more numerous spines. Merus and carpus in length and each about 0.6 the length of the ischium; propodus shorter than ischium but longer than merus or carpus.

Pleopods 1 and 2 (Fig. 6(a), (b) ) with peduncle as long as broad, inner margin with 6 coupling hooks. Endopod of pleopod 1 about 0.3 as wide as exopod, both rami with only the distal margin setose. Pleopod 2 with sabre-like appendix masculina arising 0.3 of way along inner margin and extending beyond endopod by 0.25 its length. Pleopods 3-5 (Fig. 6(c)-(e) ) with prominent suture across exopod. Endopods of pleopods 3 and 4 with subtruncate distal margin, with 9 and 6 setae respectively; endopod of pleopod 5 glabrous.

Telson (Fig. 6(f) ) as long as greatest width, posterior margin gently rounded, without spines, dorsal surface with slight longitudinal depression, and slight lateral depression at anterior end. Uropods (Fig. 4(e) ) not reaching beyond telson (Fig. 6(f) ) with peduncle very broad in lateral aspect (Fig. 4(a) ), outer margin with fringe of setae and a spine, inner margin produced along half the length of endopod. Exopod slender, 5 times as long as greatest width, tapering towards apex; inner margin with 2 spines and 7 setae, distal 0.8 of outer margin with a fringe of setae; and apical spine is present. Endopod elongate, about 3.5 times as long as greatest width, inner margin with continuous fringe of setae and 5 spines, outer margin with conspicuous indentation near apex in which lies a single spine; remainder of outer margin with 9 setae.

FEMALE: Unknown.

SIZE: 11.0 mm.

COLOUR: Tan in alcohol.

ETYMOLOGY: The specific epithet is derived from the Latin word *perplexus* (= confused).

DISTRIBUTION: Known only from the type locality.

### **Cirolana bathynella** sp. nov. (Figs. 7 & 8)

MATERIAL: From the South Australian Museum collection. 2♀♀, 47 mm x 13 mm and 45 mm x 12 mm, Tasmania. No other data.

TYPES: Holotype ♀, SAM, Reg. No. C 3829.
Paratype ♀, SAM, Reg. No. C. 3830.

TYPE LOCALITY: Tasmania.

DESCRIPTION OF FEMALE: Body smooth, elongate, slightly more than 3.5 times as long as greatest width; cephalon with anterior margin smoothly rounded, eyes narrow and elongate, slightly broader posteriorly (Fig. 7 (a) ). Clypeus broader anteriorly, anterior margin raised (Fig. 7(c) ), frontal lamina set into clypeus, posterior portion raised into a horn like projection, anterior margins narrows to an acute point.

Pereonite 1 longer than 2, pereonites 2-7 becoming progressively longer posteriorly (Fig. 7(a) ). Pereonite 1 with lateral groove; coxae 2-3 short, 4-7 produced posteriorly, those of pereonite 7 enclosing pleonites 1 and 2, each with a diagonal carina. Pleon with all segments visible, postolateral margins of pleonite 3, encompassing pleonites 4 and 5 (Fig. 7(a), (b) ).

Antennule (Fig. 7(h) ) extending to anterior margin of pereonite 1, peduncular article 3 twice as long as article 1, flagellum composed of about 24 articles, the first being the longest. Antenna (Fig. 7(i) ) with peduncular article 1 very short, articles 2 and 3 sub-equal in length as are articles 4 and 5; flagellum extends to posterior margin pereonite 5.

Mouthparts. Not markedly different from other members of the genus. Maxilliped (Fig. 8(a) ) broad, abundantly supplied with setae, endite with 2 coupling hooks and a row of about 6 plumose setae. Maxillule (Figs. 7 (g), 8(c) ) with 12 stout and one slender spine on gnathal surface of exopod. Maxilla (Fig. 8(b) ) with about 10 setae on palp and about 20 on outer lobe; endite with 11 plumose and about 14 simple setae.

Pereopods all ambulatory. Pereopod 1 (fig. 7(f) ) short, robust, with few spines or setae; propodus with 4 spines on posterior margin. Pereopod 7 (Fig. 8(h) ) with few setae, a group of spines present at each distal angle of ischium, merus and carpus as well as additional spines on the hind margins.

Pleopods with peduncle broader than long, those of pleopods 1 and 2 (Fig. 8(i) ) with 8 plumose coupling hooks and 12 plumose setae; outer margin with small lobe. Pleopod 1 (Fig. 8(e) ) with exopod as broad as endopod, but narrowing rapidly to form a subacute tip; endopod straight sided. Pleopod 3 (Fig. 8(f) ) and 4 with fringe of marginal setae on exopod, endopod only partially setose. Pleopod 5 with endopod glabrous. Inner margins of endopods of pleopods 3 and 4 with partial suture.

Telson (Fig. 7(b) ), as broad as long, slight constriction anteriorly; posterior margin broad, feebly crenulate, with setae but no spines. Dorsal surface domed with shallow median depression. Uropod with peduncle produced into an acute lobe extending a little less than halfway along inner margin of endopod. Exopod narrow about 3.5 times as long as broad, fringe of setae along entire length of outer margin and distal half of inner margin which also has 3 spines; endopod without spines, inner and hind margin setose; extends beyond endopod, posterior margin somewhat truncate.

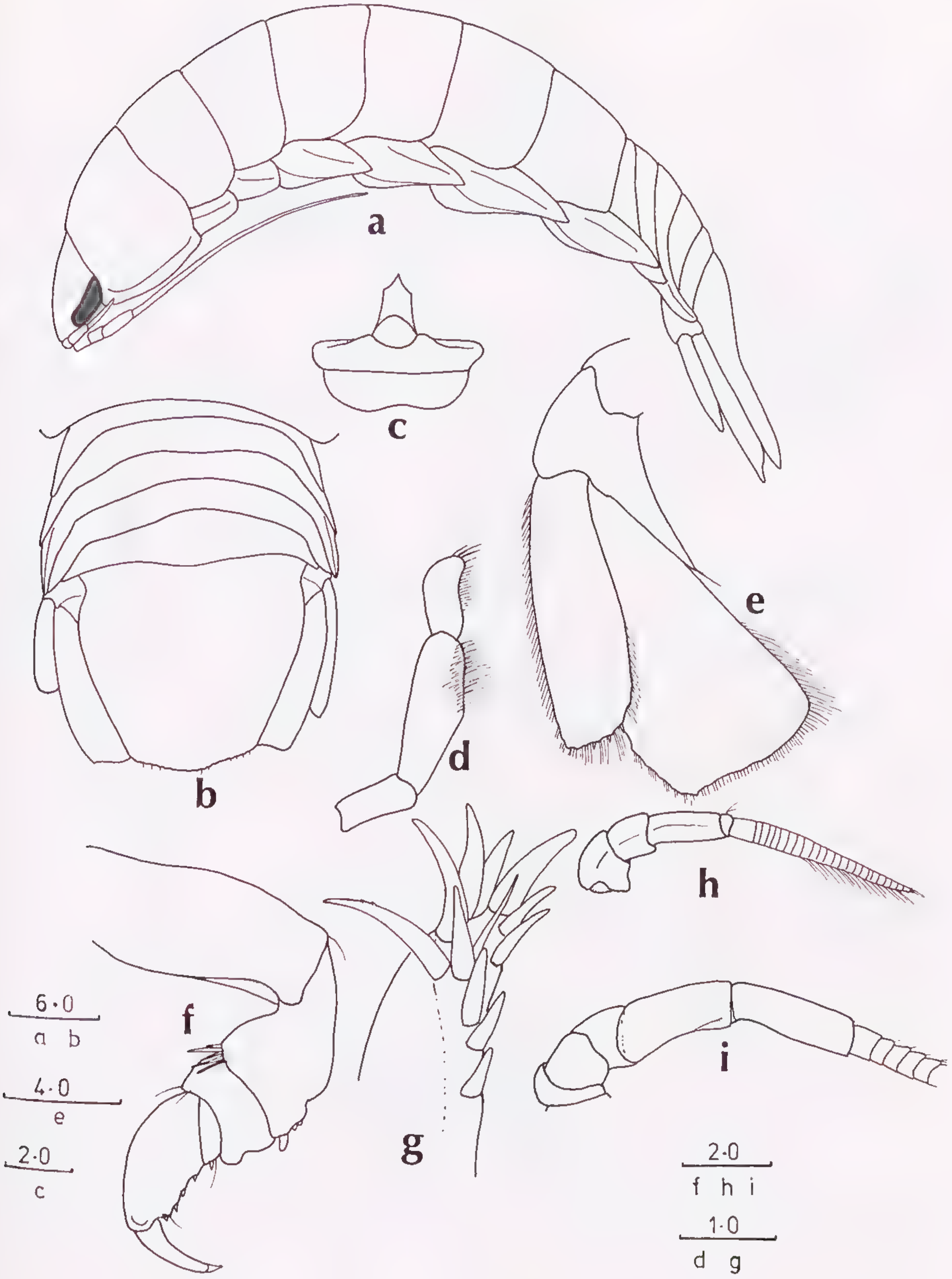

Figure 7. *Cirolana bathynella* sp. nov. **(a)**-**(c)** holotype **(d)**-**(i)** paratype **(a)** lateral view **(b)** pleon and telson **(c)** frontal lamina, clypeus and labrum **(d)** mandibular palp **(e)** uropod **(f)** pereopod 1 **(g)** gnathal surface of maxillule **(h)** antennule **(i)** antennal peduncle. Scale line, mm.

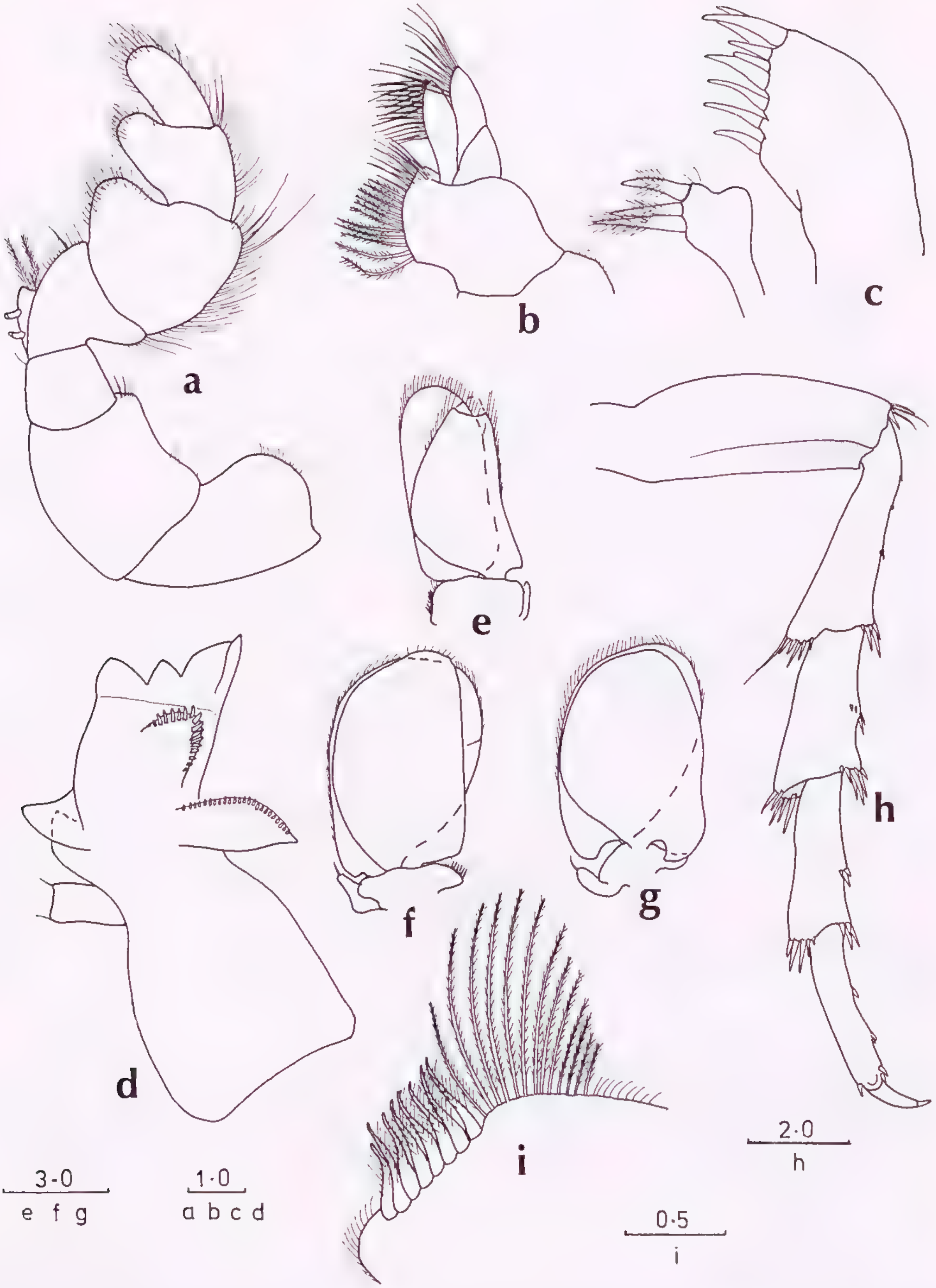

Figure 8. *Cirolana bathynella* sp. nov. All figs from paratype. **(a)** maxilliped **(b)** maxilla **(c)** maxillule **(d)** mandible **(e)** pleopod 1 **(f)** pleopod 3 **(g)** pleopod 5 **(h)** pereopod 7 **(i)** medial margin of peduncle of pleopod 1. Scale line, mm.

MALE: Unknown.

SIZE: Largest female 47 mm x 13 mm.

REMARKS: The large size of this species together with details of the antero-clypeal region, telson, uropods and pleopods immediately separate this from other species of the genus.

There are two species with which *C. bathynella* shares several characters, *C. quadripustulata* Hurley, 1957, and *Parabathynomus natalensis* Barnard, 1924, (Kensley, 1978). In all three species the telson, uropods, pleon, antennae, antennules and eyes are similar in form. Apart from the dorsal processes *C. quadripustulata* has more numerous spines on the uropods, and 4 spines on the inner lobe of the maxillule. *Parabathynomus* can be distinguished by the presence of branchial tufts on the uropods and by the produced merus of pereopod 1. Were it not for the lack of branchial tufts, *Cirolana bathynella* sp. nov. could be placed in the genus *Parabathynomus* which emphasises the closeness of that genus of *Cirolana*. Although the females are non ovigerous, it seems unlikely that they would develop branchial tufts as pereopod 7 suggests they are fully developed.

The setation of pleopods 3 and 4 is unusual for the genus. In the genus *Cirolana*.it is normal for all rami but the endopod of pleopod 5, to be setigerous. In this species the endopods of pleopods 3 and 4 are almost entirely without setae. The large number of coupling hooks on the protopods of pleopods 1 and 2 is also distinctive. Most species of the genus possess 3 or 4 as opposed to 8 in *C. bathynella*. Until the male of the species is known, it seems best to place it in the genus *Cirolana* but occupying an isolated position close to *C. quadripustulata* and the genus *Parabathynomus*.

ETYMOLOGY: The specific name is derived from the Greek word *bathos* (= deep) and alludes to its affinity to *Parabathynomus*.

DISTRIBUTION: From off the Tasmanian coast.

### **Cirolana halei** sp. nov. (Figs. 9 & 10)

MATERIAL: N.S.W. shelf, Hunter District, HDWBS stns: off Stockton Beach, 32°53′55″S, 151° 47′ 13″E, 15 m. 30.11.1975, (2 specimens); off Burwood Beach, 32° 57′ 31″S, 151°44′ 43″E, 24 m, 22.8.1975, (1). Off North Head, Sydney, SBS stn: 151°18′E, 33°49′S, 32 m, 25.5.1972(16).

TYPES: Holotype. ♂, AM Reg. No. P28695.
Paratypes. 2 ♀ specimens AM Reg. No. P23051 and 23052.
Paratypes. 4 NMV Reg. No. J684.
Paratypes. 4 SAM Reg. No. C3869.

TYPE LOCALITY: Off Stockton Beach, N. of Hunter River, N.S.W. 15 m, 30.11.1975.

DESCRIPTION OF MALE: Body smooth, about 3 times as long as broad (Fig. 9(a) ). Cephalon with small rostral point, frontal lamina (Fig. 9(c) ) broad, straight sided, pentagonal in shape.

Pereonite 1, 0.5 as long again as pereonite 2; pereonites 2 and 3 sub-equal in length and shorter than pereonites 4-7, which are also sub-equal in length. Each coxa (Fig. 9(b) ) with a carina, posterior margin of coxae 5-7 produced to a gently tapered point. Pleon short, pleonite 1 almost entirely concealed, epimera of segment 3 produced but not overlapping pleonite 4; pleonite 5 with lateral margin encompassed by pleonite 4.

Antennule (Fig. 9(g) ) with 2-articulate peduncle, article 2 longer than 1; flagellum with 6 articles, extending to anterior margin of pereonite 1. Antenna (Fig. 9(f) ) with first 3 peduncular articles short, article 3 slightly longer than 2; articles 4 and 5 sub-equal in length. Flagellum extending to posterior margin of pereonite 2.

Mouthparts. (Fig. 10(a)-(d) ) not differing notably from other members of the genus. Maxilliped (Fig. 10(a) ) with 6 and 3 setae on outer margins of palp articles 3 and 4 respectively; endite with two coupling hooks. Mandible (Fig. 10(d) ) with moderately narrow cutting edge; palp with articles 1 and 2 subequal in length.

Pereopods all ambulatory, 1-3 robust, 4-7 less so. Pereopod 1 (Fig. 9(d) ) robust, ischium with a single blunt and one acute spine on posterior distal angle; merus with 4 blunt spines and propodus with 2 acute spines one of which opposes the dactyl. Merus, carpus and propodus with dense fringe of setae along posterior margins. Dactyl with well developed secondary unguis. Pereopod 7 (Fig. 9(e) ) with very few setae. Anterior margin of basis formed into a keel-like ridge; ischium, merus and carpus with spines at distal angles; posterior margins of merus, carpus and propodus with numerous spines. Ischium and propodus subequal in length and longer than the carpus which is longer than the merus.

Pleopods (Fig. 10(e) (h) ) with marginal setae on all rami except the endopod of pleopod 5 (fig. 10(h) ). Pleopod 1 (Fig. 10(e) ) with endopod 0.66 as wide and a little shorter than exopod, tapering in distally. Pleopod 2 with appendix masculina rising basally (Fig. 10(f) ) and extending beyond inner ramus by 0.5 its length. Pleopods 3-5 with complete suture across exopod; pleopods 1-3 with 4 coupling hooks each.

Telson (Fig. 9(h) ) with sides slightly concave, dorsal surface raised, but does not form a distinct ridge; posterior margin subtruncate, armed with 8 robust spines and short setae. Uropod with single spine on external margin of peduncle and 2 spines on ventral posterior margin; endopod broad, inner margin with 5 stout spines, apex bifid, outer margin with 2 spines and a brush tipped seta, both margins with setae; exopod narrower, shorter than endopod, apex bifid; outer margin with 3 spines and a few short setae, inner margin with 3 large spines and about 8 setae.

FEMALE: As for the male, but lacking appendix masculina and the setae on pereopod 1.

SIZE: Largest female 6.0 mm. Male 5.0 mm.

COLOUR: Pale tan to cream with numerous black chromataphores.

REMARKS: This species can be identified by the combination of the following characters: the frontal lamina, the antennule, telson and uropods, pleopods 1 and 2 and the male pereopod 1. There are two species, *Neocirolana obesa* Hale 1925 and *Cirolana cranchii* var. *australiense* Hale, 1925, which show a certain similarity to this species. *N. obesa* can be distinguished by having a narrower cutting edge of the mandible, a distinct frontal lamina, a shorter antennule and by the production of pleon segment 3 to reach to the hind margin of the pleon. This last feature also separates *C. cranchii australiense* from *C. halei*. *C. cranchii australiense* is further distinguished by having more numerous spines on the uropodal rami and in having the endopod of pleopod 1 straight sided.

ETYMOLOGY: This species is named in honour of Herbert M. Hale who pioneered the study of this family in Australia.

DISTRIBUTION: Off Hunter District and Sydney coasts, from 15 m to 32 m, from fine sand.

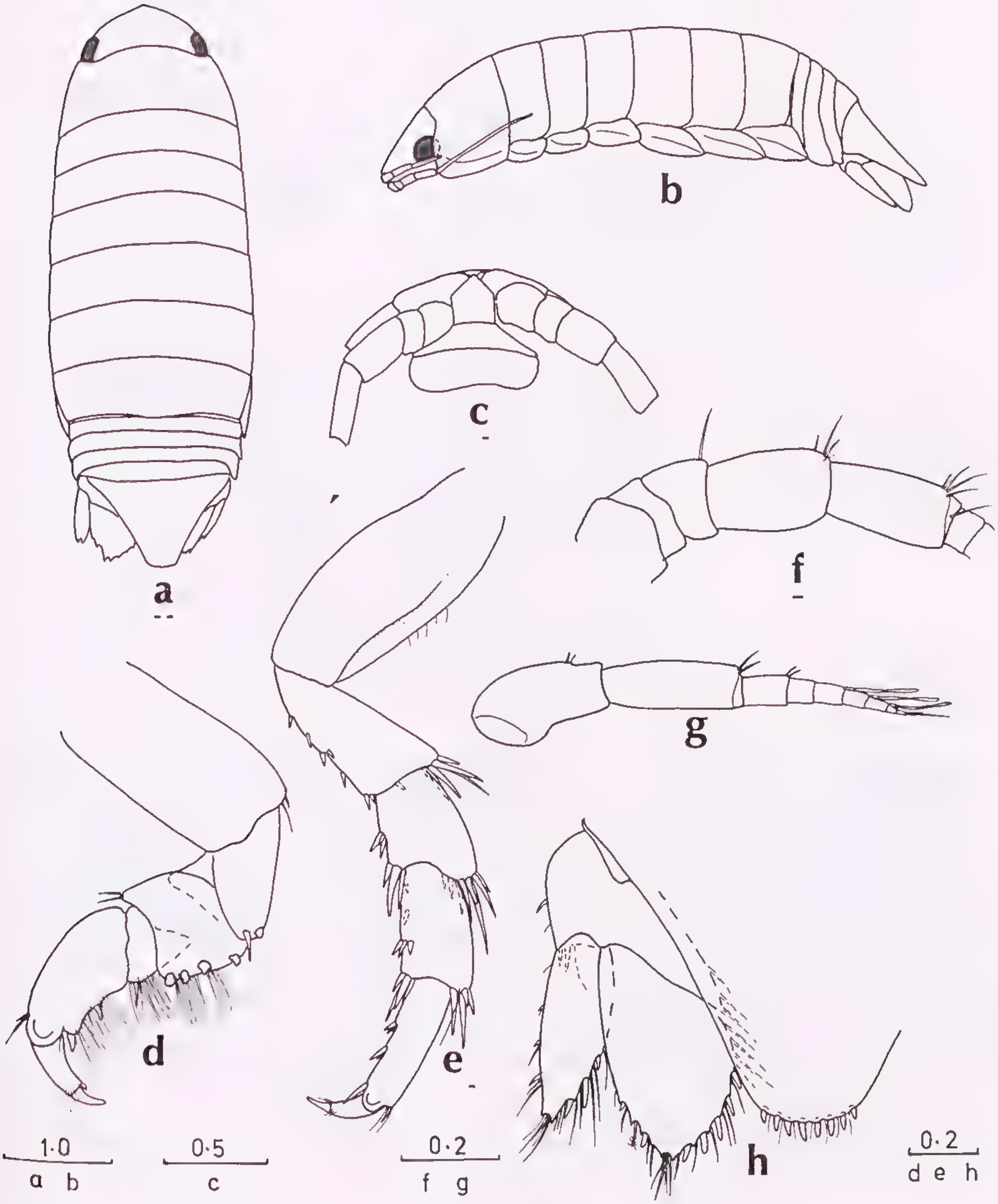

Figure 9. *Cirolana halei* sp. nov. **(a)-(c)** holotype **(d)-(h)** paratype **(a)** dorsal view **(b)** lateral view **(c)** clypeal region **(d)** pereopod 1 **(e)** pereopod 7 **(f)** antennal peduncle **(g)** antennule **(h)** telson and uropod. Scale line, mm.

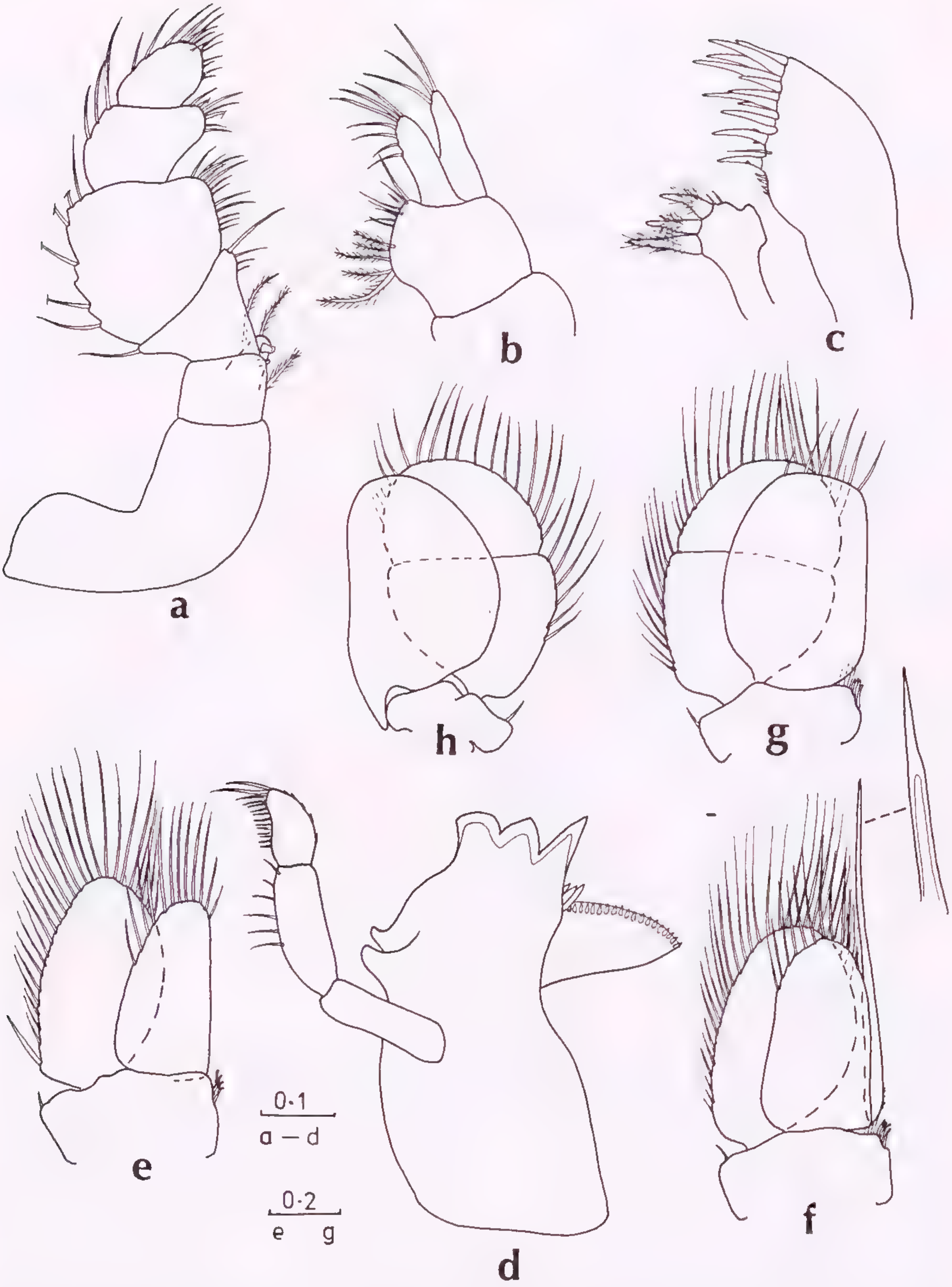

Figure 10. *Cirolana halei* sp. nov. All figs. paratype. **(a)** maxilliped **(b)** maxilla **(c)** maxillule **(d)** mandible **(e)** pleopod 1 **(f)** pleopod 2 **(g)** pleopod 4 **(h)** pleopod 5. Scale line, mm.

**Cirolana triloba** sp. nov. (Figs. 11 & 12)

MATERIAL: NSW shelf, off Malabar, Sydney, SBS stns: 151°19′E,33°57′S, 66 m, 19.5.1972 (2 specimens) and 71 m (4); 151°17′E,33°58′S, 66 m, 30.1.1974 (1).

TYPES: Holotype. AM Reg. No. P. 28696
Paratypes. AM Reg. No. P 22881 (♂and♀), P 22882 (♀) and P 28697 (2♀♀).
Paratype. NMV Reg. No. J686

TYPE LOCALITY: Off Malabar, Sydney, N.S.W., 71 m, 19.5.1972.

DESCRIPTION OF MALE: Body robust, surface coarse, a little more than 2.5 times as long as broad. Cephalon with an indistinct tubercle on dorsal surface. Clypeus (Fig. 11(c) ) narrow; frontal lamina (Fig. 11(c) ) broad with anterior projection meeting a small process separating the antennules.

Pereonite 1 more than twice the length of pereonite 2 (Fig. 11 (a) ); pereonites 3-6 sub-equal in length and slightly longer than pereonites 2 and 7; pereonites 3-7 with impressed line on posterior portion, those on pereonites 6 and 7 being more prominent (Fig. 11(b) ); lateral margin of pereonite 1 with one complete and one partial longitudinal line. Coxae 2 and 3 not produced, each with a longitudinal carina, coxae 4-7 produced, each with an oblique carina. Pleonite 1 almost entirely concealed by pereonite 7, pleonite 4 with 4 inconspicuous tubercules, pleonite 5 with 3 conspicuous tubercules; lateral margin of pleonite 3 produced to the posterior of pleon, partially overlapping pleonite 4 which in turn encompasses the lateral margin of pleonite 5.

Antennule peduncle (Fig. 11(f) ) 2-articulate, no clear suture visible on the first article; flagellum of 6 articles, article 1 longest. Antenna (Fig. 11(g) ) with peduncular articles 1-3 short, article 5 longer than 4; flagellum extends to posterior margin of pereonite 4.

Mouthparts. (Fig. 12(a)-(d) ) typical of the genus. Maxilliped broad, endite with 2 coupling hooks (Fig. 12(a) ). Cutting edge of mandible not narrow (Fig. 12(c) ).

Pereopods all robust and ambulatory; pereopods 1-3 shorter and more robust than 4-7. Pereopod 1 (Fig. 11(h) ) with stout basis; ischium and merus with anterior margins only slightly produced posterior margin of ischium and carpus with 1 and 5 large blunt spines respectively, propodus with 3 acute spines; posterior margins of carpus, merus and propodus with dense fringe of setae. Dactyl (Fig. 11(h), detail) with well developed robust secondary unguis. Pereopod 7 virtually without setae (Fig. 11(j) ), anterior margin of basis slightly produced, anterodistal angles of ischium, merus and carpus with group of spines, posterior margins of ischium, merus and carpus with numerous spines. Merus and carpus sub-equal in length and shorter than propodus which is shorter than ischium. Dactyl with secondary unguis.

Pleopods with marginal setae on all rami but the endopod of pleopod 5. Complete suture on pleopods 3 (Fig. 12(g) ) to 5. Endopod of pleopod 1, narrow tapering towards apex (Fig. 12(e) ). Pleopod 2 (Fig. 12(f) ) with appendix masculina arising basally, twice the length of the endopod, apex narrowing to a point.

Telson with posterior margin truncate (Fig. 11(a) ) armed with 6 spines and as many short setae. There is a median irregularly tuberculate ridge (Fig. 11(b) ) running 0.66 the length of the telson. Uropod with endopod broad, inner margin serrate, each notch provided with a stout spine; apex bifid, outer margin with 2 spines and one brush tipped seta; exopod about 0.66 as wide and slightly shorter than endopod, inner and outer margins each with 3 stout spines, those on outer margin being smaller. Uropods do not

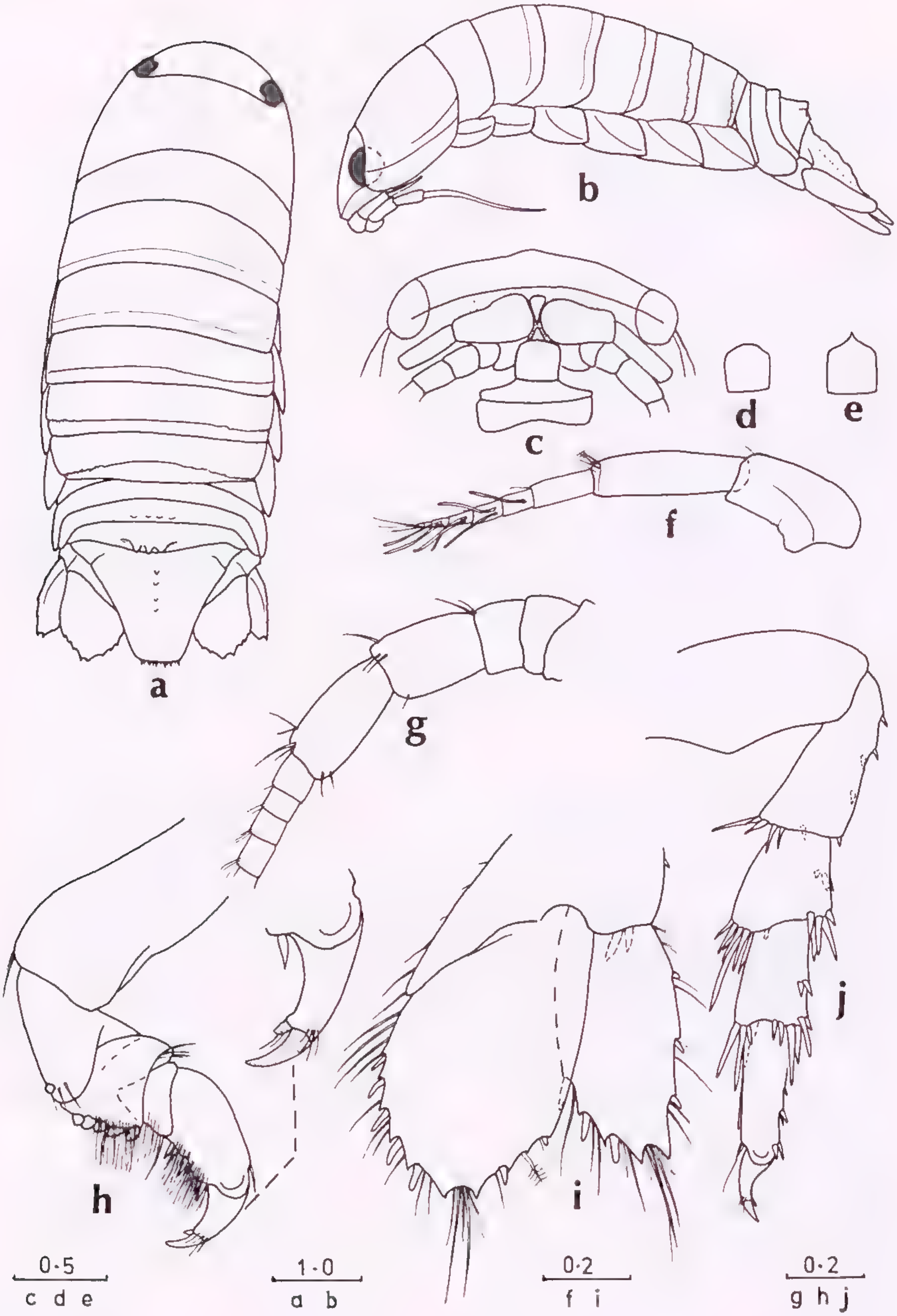

Figure 11. *Cirolana triloba* sp. nov. **(a)**-**(c)** holotype **(d)**-**(j)** paratype **(a)** dorsal view **(b)** lateral view **(c)** clypeal region **(d)**, **(e)** variations, frontal lamina, type series **(f)** antennule **(g)** peduncle of antenna **(h)** pereopod 1 **(i)** uropod **(j)** pereopod 7. Scale line, mm.

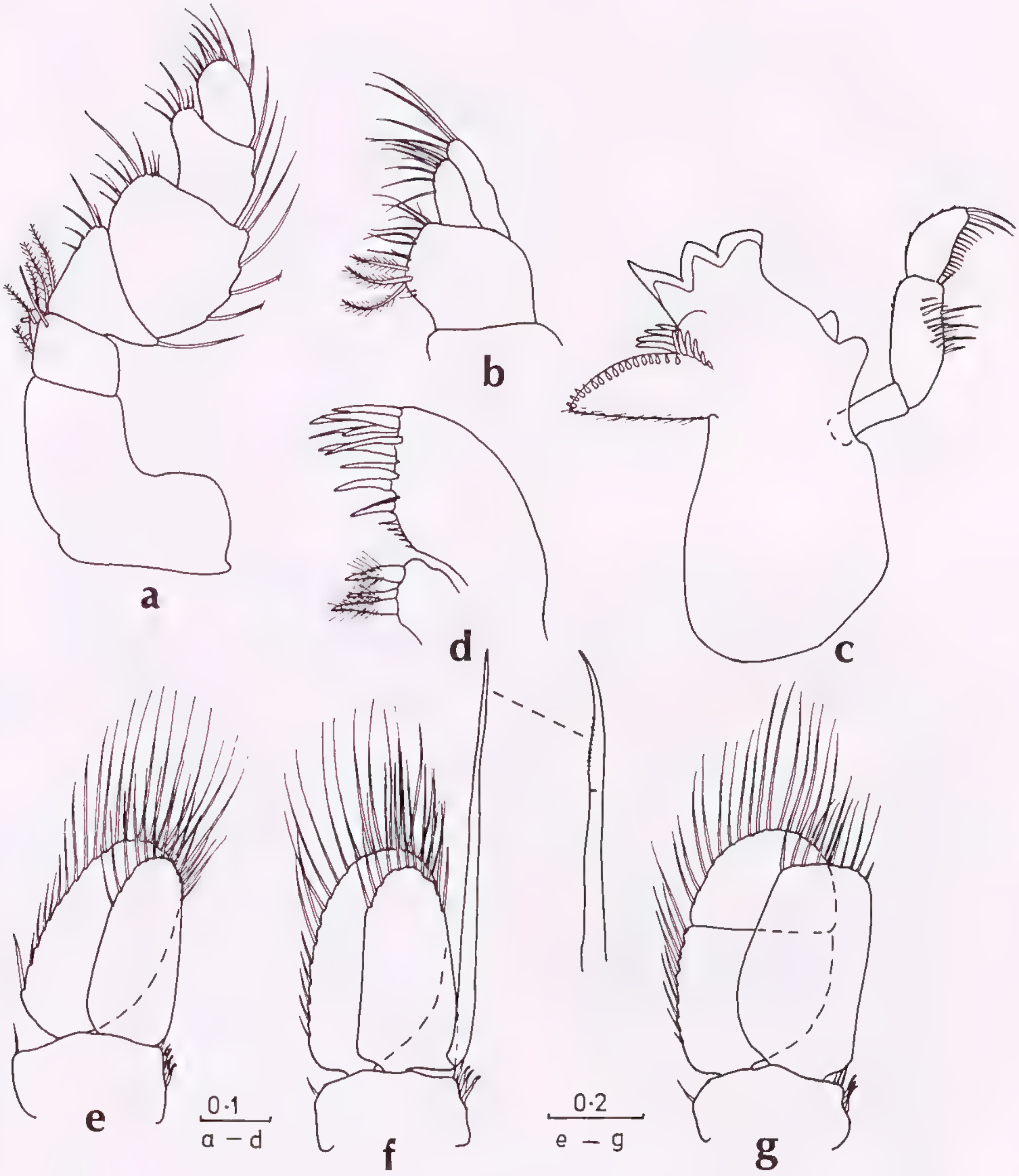

Figure 12. *Cirolana triloba* sp. nov. All figs. from paratype **(a)** maxilliped **(b)** maxilla **(c)** mandible **(d)** maxillule **(e)** pleopod 1 **(f)** pleopod 2 **(g)** pleopod 4. Scale line, mm.

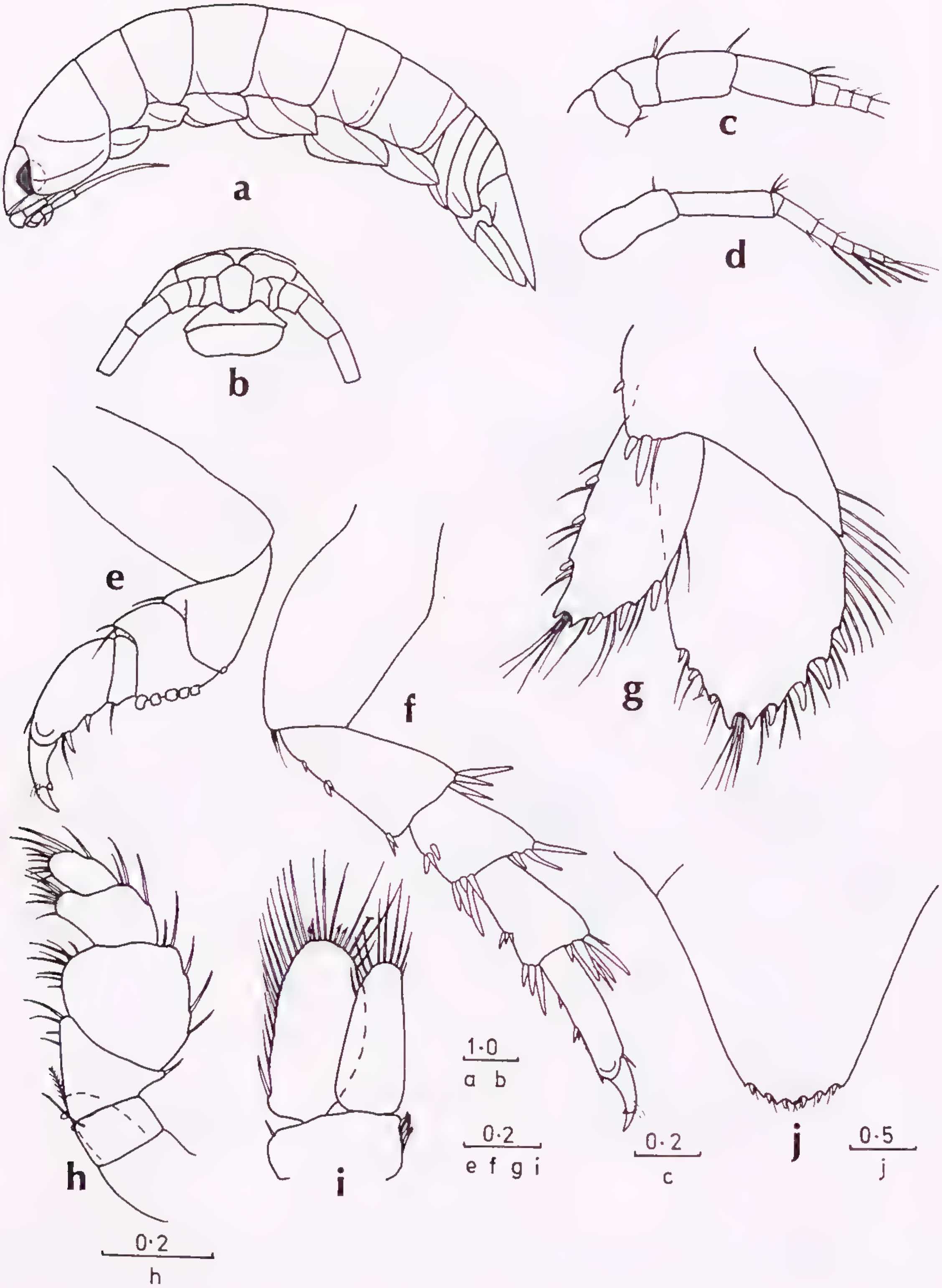

Figure 13. *Cirolana furcata* sp. nov. All figs from holotype. **(a)** lateral view **(b)** clypeal region **(c)** antennal peduncle **(d)** antennule **(e)** pereopod 1 **(f)** pereopod 7 **(g)** uropod **(h)** maxilliped **(i)** pleopod 1 **(j)** telson. Scale line, mm.

extend beyond apex of telson.

FEMALE: Generally similar to male. Sculpting of pleon and telson present, but less conspicuous. The fringe of setae on pereopod one and the male sexual characters are absent.

SIZE: Largest male 6.5 mm; female 6.0 mm.

COLOUR: Tan to cream in alcohol.

REMARKS: This species can be separated from all others of the genus by the ornamentation of the pleon and telson.

ETYMOLOGY: The specific name is derived from the latin word *lobatus* (= lobed).

DISTRIBUTION: Known only from off Malabar, NSW at depths from 66 m to 71 m, fine sand and gravel sand bottom.

### **Cirolana furcata** sp. nov. (Fig. 13)

MATERIAL: NSW shelf, off North Head, Sydney, SBS stn: 51°18′E,33° 49′S, 32.9 m, 23.5.1978, (1 ♀ and 1 manca).

TYPES. Holotype. AM Reg. No. P 28694.
Paratype. manca AM Reg. No. P 22874

TYPE LOCALITY: Off North head, Sydney, N.S.W. 32 m, 23.5.1972.

This species and the next two are in most characters extremely close to C. *triloba* sp. nov. and the descriptions given will deal mainly with the differences. Where not mentioned, a character can be assumed to be the same as, or not differing significantly from C. *triloba*.

DESCRIPTION OF FEMALE: Cephalon without tubercule. Pereonites 1-5 without transverse impressed lines (Fig. 13(a) ). Frontal lamina slightly broader anteriorly, anterior margin obscurely 3-sided; clypeus formed into two projecting triangular process, one on each side of frontal lamina (Fig. 13(b) ).

Antennule peduncle with articles 1 and 2 fused (Fig. 13(d) ), article 3 longer than fused articles 1 and 2. Antenna (Fig. 13(c) ) with first 3 peduncular articles short, articles 4 and 5 sub-equal in length; flagellum extends to posterior of pereonite 2.

Mouthparts. As for the preceding species except for outer margin of maxilliped palp articles (Fig. 13(h) ) which have fewer and shorter setae.

Pereopod 1 (Fig. 13(e) ) with two acute spines on posterior margin of propodus.

Pleopods as for the preceding species.

Telson (Fig. 13(j) ) with subtruncate hind margin with 6 stout spines and central pair of simple setae. Dorsal surface is domed, but without any sculpture. Uropods (Fig. 13(g) ) with endopod armed with 4 and 3 spines on outer and inner margins respectively; endopod with 3 spines each on inner and outer margins. Both rami with bifid apex.

MALE: Unknown.

SIZE: 10 mm.

COLOUR: Cream in alcohol.

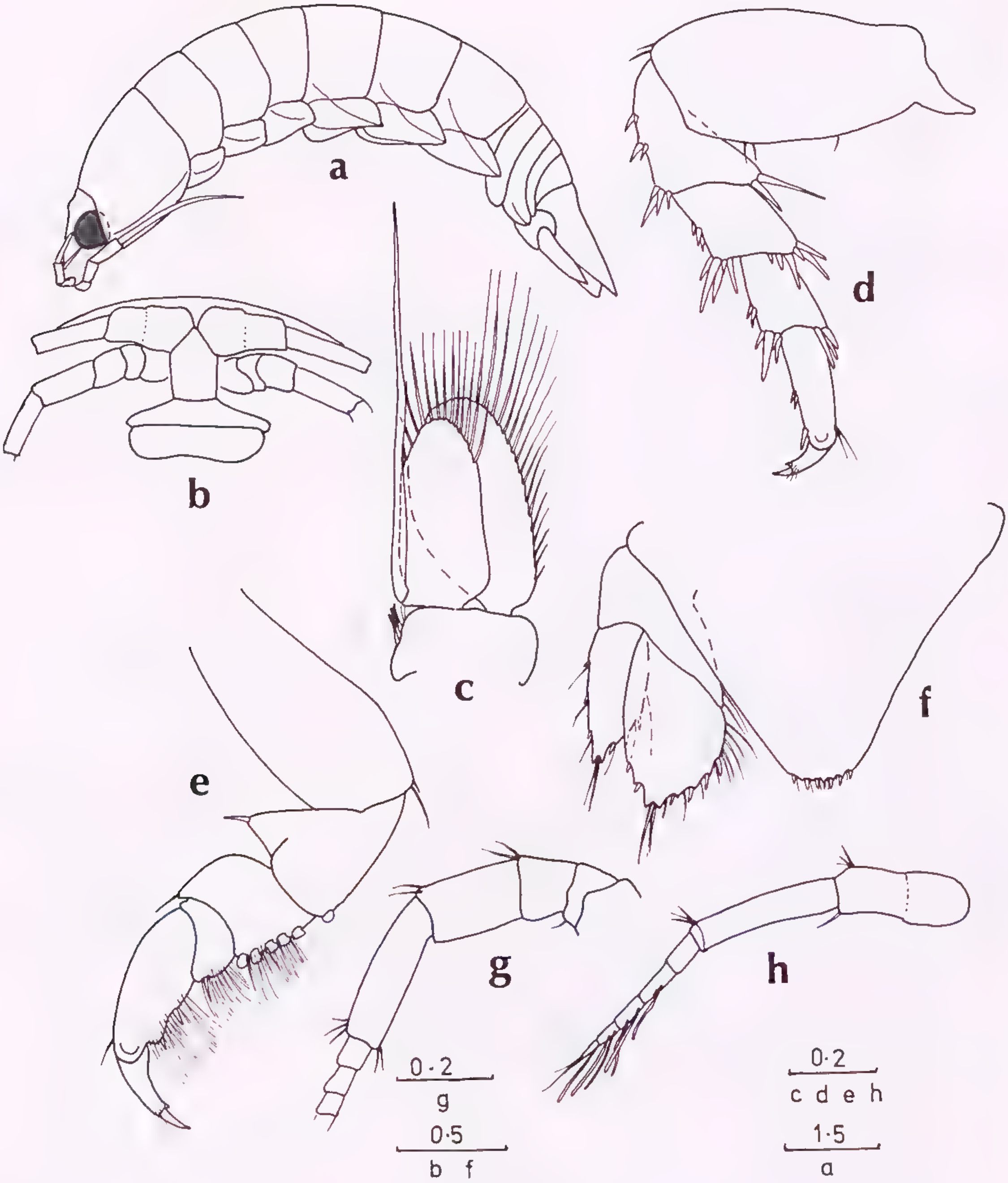

Figure 14. *Cirolana similis* sp. nov. All figs holotype. **(a)** lateral view **(b)** clypeal region **(c)** pleopod 2 **(d)** pereopod 4 **(e)** pereopod 1 **(f)** telson and uropod **(g)** antennal peduncle **(h)** antennule. Scale line, mm.

REMARKS: This species shows a close resemblance to the previous species from which it can easily be distinguished by the unique clypeus present on both specimens which also separates it from all other *Cirolana* species.

ETYMOLOGY: The specific epithet is taken from the Latin word *furcatus* (= cloven or branched), and alludes to the shape of the clypeus.

DISTRIBUTION: Known only from the type locality.

### **Cirolana similis** sp. nov. (Fig. 14)

MATERIAL: NSW shelf, off North Head, Sydney, SBS stn: 51°19′E, 33°57′S, 32 m, 1973 (1♂, 15♀♀).

TYPES: Holotype. AM Reg. No. P 28698
Paratypes. AM Reg. No. P 22883
Paratypes. NMV Reg. No. J685
Paratypes. SAM Reg. No. C3870

TYPE LOCALITY: Off Malabar, Sydney, N.S.W. 32 m, 1973.

DESCRIPTION OF MALE: Pereonites without impressed lines or sculpture. Dorsal surface of cephalon with a single distinct tubercule (Fig. 14(a) ). Clypeus narrow, frontal lamina about twice as long as broad, pentagonal in shape (Fig. 14(b) ).

Antennule (Fig. 14(h) ) with articles 1 and 2 fused, suture just visible; article 3 longer than combined lengths of articles 1 and 2. Antenna (Fig. 14(g) ) with articles 1-3 short; article 3 half as long again as article 4.

Mouthparts. Not differing notably from those of *C. triloba*.

Pereopods much the same as in the previous two species. Pereopod 1 (Fig. 14(e) ) with dense fringe of setae on posterior margin of merus, carpus and propodus; two spines only on posterior margin of propodus.

Pleopods as for *C. triloba*. Pleopod 2 (Fig. 14(c) ) with appendix masculina twice the length of inner ramus.

Telson (Fig. 14(f) ) with 6 spines on posterior margin. Uropods similar to preceding two species. Outer margin of endopod with 2 spines. Uropods extend a short way beyond telson.

FEMALE: Lacks the male sexual characters and the setae of pereopod 1. Cephalic tubercule less conspicuous, but present. Otherwise as for the male.

SIZE: Largest female 10 mm.

COLOUR: Cream in alcohol.

REMARKS: This species can be separated from *C. triloba* by the total lack of sculpture of the pleon and telson, by the difference in frontal lamina, and by the lack of impressed lines on the pereon segments. The clypeus, frontal lamina and cephalic tubercule separate this species from *C. furcata* sp. nov. and *C. halei* sp. nov.

ETYMOLOGY: The epithet, is the Latin word *similis* (= like) which alludes to the species' resemblance to *C. triloba*, and *C. halei*.

DISTRIBUTION: Known only from the type locality.

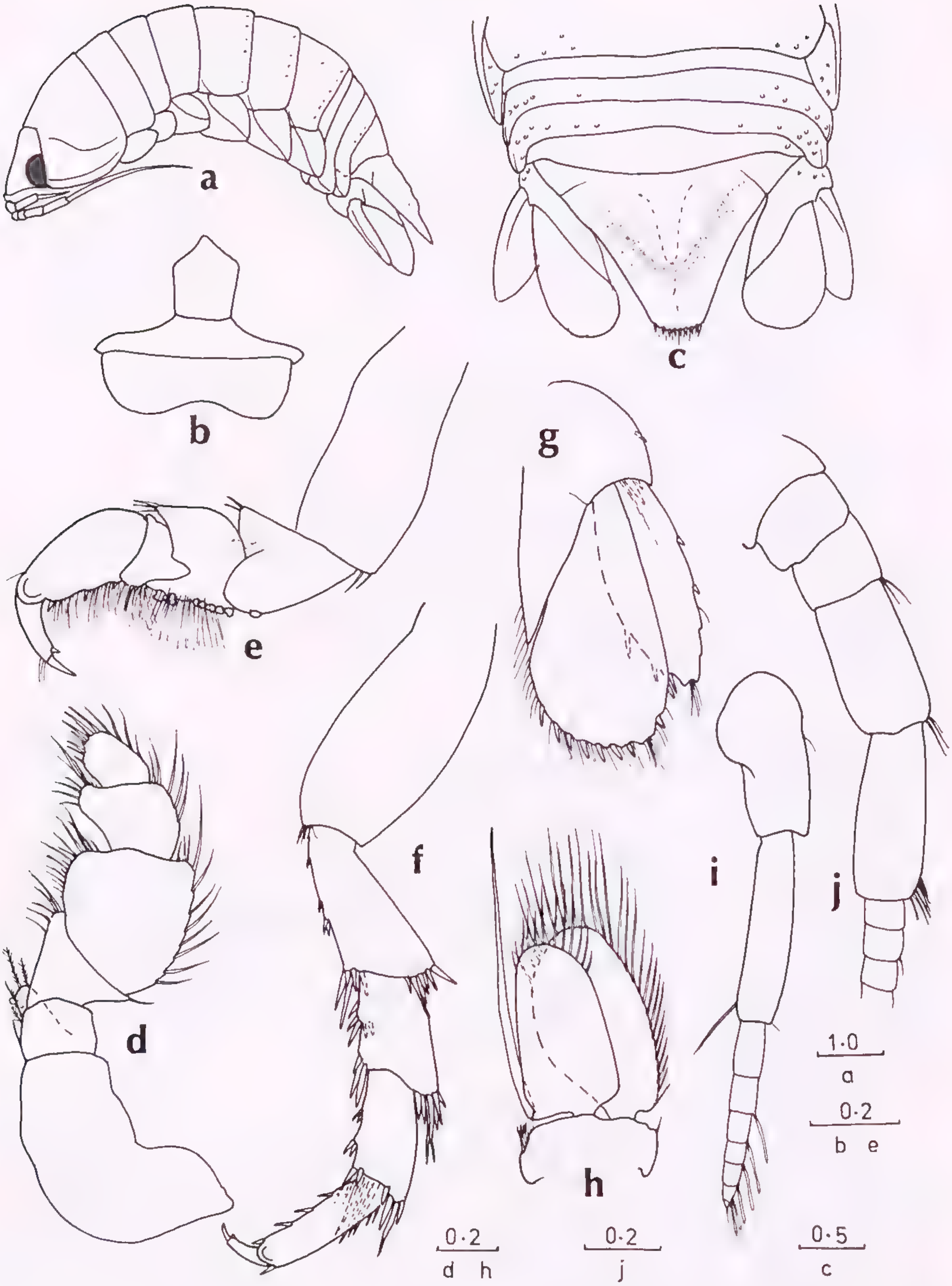

Figure 15. *Cirolana victoriae* sp. nov. Holotype. **(a)** lateral view **(b)** frontal lamina, clypeus and labrum **(c)** pleon and telson **(d)** maxilliped **(e)** pereopod 1 **(f)** pereopod 7 **(g)** uropod **(h)** pleopod 2 **(i)** antennule **(j)** antenna. Scale line, mm.

### **Cirolana victoriae** sp. nov. (Fig. 15)

MATERIAL: O. A. Sayce Collection, P. 25.7.11. Shoreham, Western Port, Victoria, 31.3.1902. Coll. S. W. Fulton. No other data.

TYPES: Holotype.♂; NMV Reg. No. J661

TYPE LOCALITY. Western Port, Victoria, 31.3.1902.

DESCRIPTION OF MALE: Pereonites without impressed lines, but dorsal surfaces coarsely pitted. Interocular carina present. Frontal lamina pentagonal (Fig. 15(b) ).

Antennule biarticulate, article 2 distinctly longer than article 1; flagellum short, composed of 7 articles.

Mouthparts. As for the preceding species, except maxilliped (Fig. 15(d) ) with rather more setae on external margins of maxilliped palp than in *C. triloba*.

Pereopods basically similar to previous three species. Pereopod 1 (Fig. 15(e) ) with 3 spines on palm of propodus. Pereopod 7 (Fig. 15(f) ) with numerous spines on distal margins of merus and carpus; propodus with 3 spines along posterior margin.

Pleopods same as *C. triloba*.

Telson with dorsal region raised into an irregular ridge, not distinct in dorsal view (Fig. 15(c) ), posterior margin with 8 spines. Uropods (Fig. 15(g) ) with apices not as markedly bifid as in preceding species; endopod rounded, 7 spines on inner margin, 2 on outer; exopod with 3 spines on inner margin, 4 on exterior margin.

FEMALE: Unknown.

SIZE: 7.1 mm.

COLOUR: Cream, without chromatophores in alcohol.

REMARKS: This species can be separated from *C. triloba* by the lack of pleonal tubercules, shape of the frontal lamina and the far more rounded uropods. This last character also separates *C. victoriae* sp. nov. from *C. halei*, *C. furcata* and *C. similis*.

ETYMOLOGY: The specific name derives from Victoria, the state from which the specimen was taken.

DISTRIBUTION: Known only from the type locality.

## DISCUSSION

The systematics of *Eurydice acuticadua* sp. nov., *E. spenceri* sp. nov., *Orphelana* gen. nov., and *Cirolana bathynella* sp. nov. have been discussed under the remarks for each species. Of the other *Cirolana* species described, *C. halei, C. triloba, C. furcata, C. similis* and *C. victoriae* appear to form a distinct group allied to *Neocirolana* on the one hand and the *C. cranchii/C. australiense* group on the other.

The species *C. halei, C. triloba, C. similis* and *C. victoriae* all have a setose merus, carpus and propodus on pereopod 1 of the male. This character has apparently not been recorded in any other members of the genus except for *C. cranchii* var. *australiense* and was figured but not mentioned by Hale (1925). When Naylor (1961) later elevated this variety to species rank, no mention was made of this character. Furthermore, this character has not been described for *C. cranchii* (Hansen, 1890; Monod, 1976, Nordenstam, 1946) in Europe nor *C. parva* Hansen, 1890, (Monod, 1930; 1933;

Richardson, 1905). It seems quite probable therefore that the animal described by Hale as var. *australiense* is both distinct from *Cirolana parva* and *Cirolana cranchii*, but at the same time is not the animal described by Naylor (1962). These seven species seem to form a natural group within the genus *Cirolana*.

The other point worthy of mention is the number and arrangements of the antennal peduncle articles. It is clear that in the species which have a biarticulate antennular peduncle that there has been a coalescence of the first and second articles. If one accepts that the small terminal article mentioned by Jones (1976 p.211) is a true article then numerous species of *Cirolana* would have to be considered as having a 4-articulate antennule peduncles. Amongst the species of *Cirolana* there is a complete range of fusion of the first articles from freely articulating, to non articulated but with a suture present, and then to total fusion of the first two articles.

## ACKNOWLEDGEMENTS

I express my thanks to Dr J. K. Lowry of the Australian Museum, Sydney; Dr W. Zeidler of the South Australian Museum, Adelaide; Dr G. C. B. Poore, formerly of the Marine Studies Group, Melbourne, now at the National Museum of Victoria, Melbourne; Dr Roy Oleröd of the Stockholm Museum of Natural History, Sweden, and Mr W. Seed of the Royal Melbourne Institute of Technology, Victoria. It is on material provided by these individuals that this report is based. I also thank Dr D. A. Jones of the Marine Science Laboratories at Menai Bridge, U.K. for his comments on an early draft of this paper.

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Manuscript accepted for publication 21 February, 1980.

# GUIDE TO AUTHORS

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### Tables

Tables should be typed on separate sheets and numbered in Arabic numerals. Headings should be

# ON THE PAPUAN *ELOCOBDELLA NOVABRITANNIAE*, THE OCEANIAN *ABESSEBDELLA PALMYRAE* (HAEMADIPSOIDEA: DOMANIBDELLIDAE), AND AN OCEANIAN BARBRONID (HIRUDINEA).[1]

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LAURENCE R. RICHARDSON
4 Bacon St., Grafton, N.S.W. Australia

## SUMMARY

Generic definitions and detailed descriptions are given for the two domanibdelline land-leeches. An analysis of the nature of the barbronids indicates: separation of these from the Erpobdellidae s.l.; division into Australian and oriental groups; and association of the oceanian barbronid with the group of the Australian Region. It is noted that the characteristic strepsilaematous pharynx is formed by transposition of the ridges, not by torsion.

## INTRODUCTION

This paper gives definitive descriptions of two land-leeches which were briefly characterized and named in the demonstration (Richardson, 1975) of a systematization for land-leeches within a Superfamily Haemadipsoidea, also such detail as can be taken from specimens of the first barbronid leech known in Polynesia.

Coming from islands with a wide oceanic separation, the two land-leeches differ in the level of annulation on the somites of the middle series: *Elocobdella novabritanniae* of New Britain, a high island between the Solomon Group and New Guinea, incomplete 7-annulate; *Abessebdella palmyrae* of Palmyra Island, a coral atoll at the northern end of the Line (Outlying) Group in Polynesia, 5-annulate. Both possess a high level of annulation on the anterior and posterior series of somites which is a characteristic feature of many in the Domanibdellinae, others having a high level of annulation only on the anterior or the posterior series (Richardson, 1975).

The subfamily is centred on the New Guinea Archipelago and has partial extensions into Borneo, Celebes, the Philippines, Malay Peninsula, the Australian Northern Territory, and previously was known in Oceania only in the 5-annulate *Fijibdella bilobata* (Moore, 1946) of Fiji, based on a single specimen 10.0 mm long. The only other land-leech known in Oceania is the 4-annulate *Samoabdella minuta* (Blanchard, 1917), Leiobdellinae, based on three specimens from Samoa, the largest 6.0 mm long.

Moore described the annuli of the posterior series in *bilobata* as "very irregular and much jumbled" on the dorsum, an erratic areolation as shown here on the dorsal aspect of xxvi and xxvii in the holotype of *A.palmyrae* (Fig. 1,B), which is somewhat similar to the areolation shown on the ventral aspect of v, vi, and vii, in the holotype of *E.novabritanniae* (Fig. 2,I). There was no erratic areolation in the paratype or smaller specimens of *palmyrae*.

A revised key to the Families and Subfamilies in the Haemadipsoidea is given (Richardson, 1978), and a key to the known 5-annulate domanibdellines (1977b). Incomplete 7-annulate domanibdellines are known to me also in specimens from Rabaul,

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[1] A study collateral to researchers on Australian freshwater and terrestrial leeches supported by an award from the Australian Research Grants Committee.

Records of The Australian Museum, 1981, **Vol. 33 No. 14**, 673-694, Figures 1-4.

the Solomon Islands, and eastern New Guinea; but these are unsuitable for description and the group cannot be assembled at this time.

The barbronid was collected on Palmyra Island. The specimens are not in good condition, but sufficient detail can be taken which along with an analysis of the present knowledge of barbronids indicates a separation of barbronids from the Erpobdellidae s.l., division of the barbronids into an Oriental group and an Australian group, and association of the Palmyra barbronid with the barbronids of the Australian Region.

Palmyra Island provides the most easterly record for the Haemadipsoidea and for barbronids of the Australian group; and the first record for land-leeches and barbronids on an atoll.

The presence on Palmyra of two very different kinds of freshwater dependent leeches, with parallels elsewhere, indicates a dispersal process available to both, and independent of the sanguivorous habit.

Palmyra and other islands in the Out-Lying Group of the South Pacific Islands, are recognised as having been frequently visited by the Polynesians of the Hawaiian Islands.

Transport by man has been proposed as a means for the passive dispersal of freshwater leeches. There are no land-leeches in the Hawaiian Islands and the known barbronids in those islands belong to the Oriental group.

There is no support for this proposal in the freshwater dependent leeches on Palmyra Island.

### Genus **Abessebdella** Richardson 1975

1st nephropores labial, lateral to the ocular areolae of iv, v; duognathous; no salivary gland papillae; vi incomplete 4-annulate, ($b_5+b_6$) above, $a_3$ below; vii to xxiii complete 5-annulate; xxiv 4-annulate; xxv essentially 3-annulate; xxvi, xxvii 3- (?2-) on the dorsum and 2-annulate on the lateral aspects; 9 (10) annuli on the dorsum between xxiii $a_2$ and the anus; no defined auricle; the 17th nephropores at the base of a deep pit; no lambertian organs; no ejaculatory bulbs; median regions of the reproductive systems, the male amyomeric, mesomorphic, the female with the recurrent limb slightly shorter than the procurrent limb; genital pores, xi $b_5/b_6$, xii $a_2/b_5$. Oceania.

TYPE SPECIES: *Abessebdella palmyrae* Richardson 1975. Palmyra Island.

### **Abessebdella palmyrae** Richardson 1975, p.126.
Figs. 1, 2.

Holotype: Total length, 16.0 mm. Palmyra. Leeches crawling on *Tourefortia* near shore. Coll. D. Mitchell, June 13, 1935. Dissected. B.P. Museum acc. 2083

Paratype: Total length 17.0 mm. Same location, date, collector, as type, dissected; deposited Australian Museum, Sydney, Coll. No. W. 7217.

Additional Material: See below.

The following description is taken from the holotype.

GENERAL FORM: Fig. 1C. Preserved, contracted with the annuli compressed; small, heavy-bodied, the dorsum transversely convex; the venter shallowly concave; margins obtusely rounded; the maximum width at the level of the anterior margin of the posterior sucker which is narrower than the maximum width of the body. The margins converge very gradually anteriorly from the widest region to the obtuse anterior sucker; more abruptly posteriorly to the wide base of the posterior sucker.

The posterior sucker is very heavy, strongly muscular, and in life would be much wider than the body.

There is no indication of a groove or other separation of the dorsal aspect of the posterior end of the body and the dorsum of the sucker, the two continuous, but separated by a groove laterally.

Total length, 16.0 mm; at v/vi, 1.0 mm from the end of the anterior sucker, the width 2.0 mm; at 4.0 mm, the width 4.0 mm, depth 2.0 mm; at 9.0 mm, the width 6.0 mm, depth 2.5 mm; at 12.0 mm, the width 5.0 mm; at 14.0 mm, the width 4.5 mm; the ventral face of the posterior sucker slightly longer (4.5) than wide (4.2 mm).

COLOUR: Preserved in alcohol, faded, generally pale off-white. Under magnification, the dorsum immaculate, very faintly brownish along its length; the margins, white, continuous with the white venter; the dorsum and venter of the posterior sucker, white, immaculate.

PATTERN: Fig. 1C. Very vaguely indicated: a median dorsal contrast stripe from in the ocular arch to the anus, the stripe relatively narrow but occupying the full width of the median field.

A broad dark band with a narrow darker medial margin, on each side of the median stripe occupies the line of the paramedian sense organs, the paramedian field, and extends laterally to beyond the level of the line of the nephropores, i.e. enters and appears to terminate in the lower portion of the marginal field. The bands extend the full length of the body.

There are very faint indications on the anterior half of the body of elongate patches in each of the dorsal bands, as: an inner row (two or ? three patches) medial in the paramedian field, and a second row lateral in the paramedian field or possibly in the intermediate field. The patches are of the length of a somite.

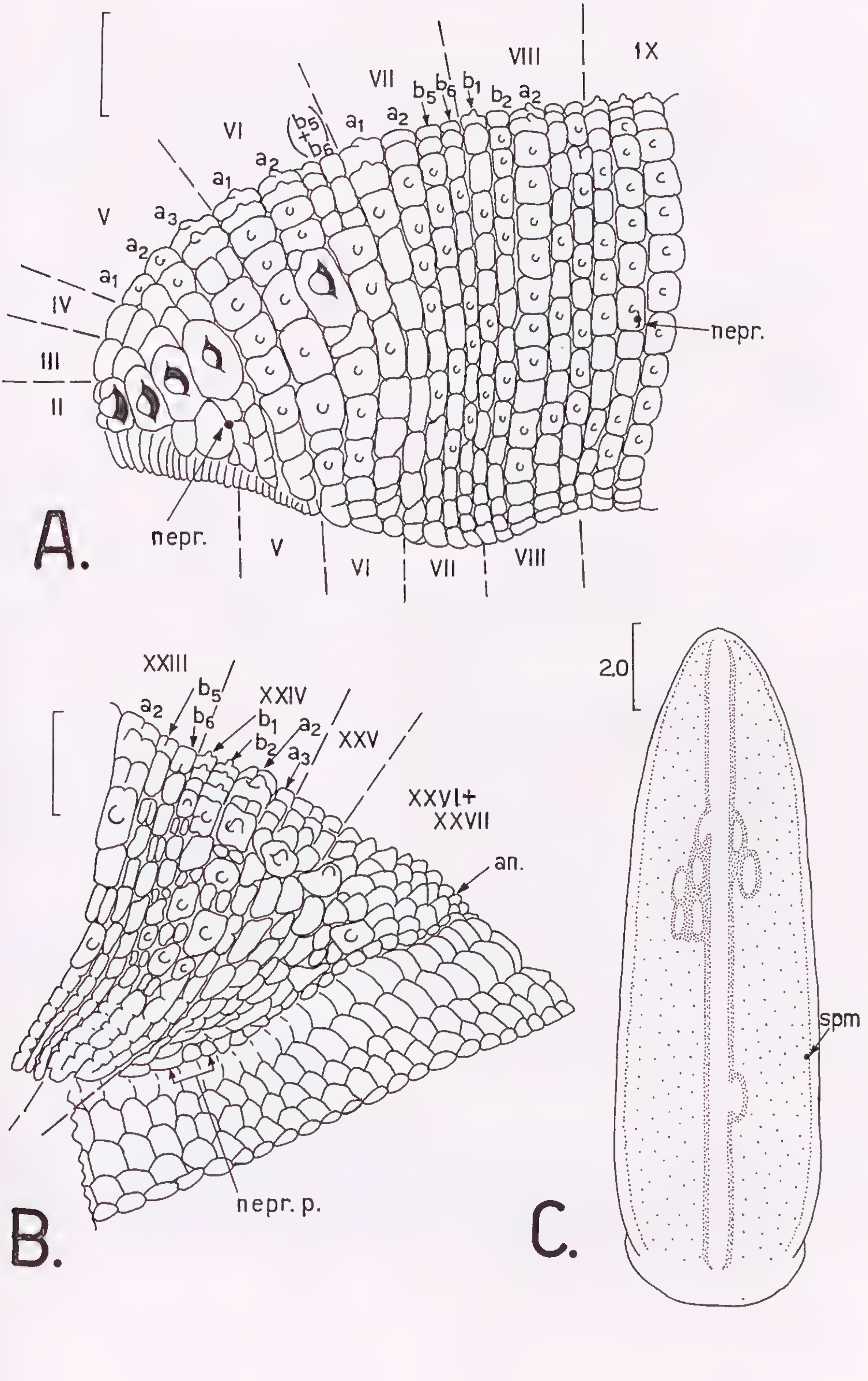
ANNULATION: Fig. 1A, B; 2D, E. Contracted so that the interannular furrows are narrow, deep; annuli strongly areolate; intersomital and interannular furrows, equivalent; somital limits not directly recognizable; somital sense organs generally obscure, the longitudinal lines of sense organs and the fields not generally definable with confidence; nephropores minute, on or near the posterior edge of the annulus and separated from the following furrows by a narrow fold of skin, the fold sometimes elevated to appear as a rounded low mound bridging between the nephroporic annulus and the following annulus.

No indication of a preocular somite i between the 1st pair of eyes and the fimbriated fold forming the anterior margin of the sucker; eyes large, protrudent, each in a large ocular areola; somite ii with the 1st pair of eyes assessable as partially 2-annulate, a single pair of reduced transverse areolae in tandem between the ocular areolae; iii, uniannulate, with 3 areolae between the oculars; iv, uniannulate, 5 areolae between the oculars; the 1st nephropores at iv/v, lateral to the ocular areolae; v, complete 3-annulate, $a_1=a_2 < a_3$, $a_1$ and $a_2$ each with 6 areolae between the oculars, the 4th eyes in $a_2$, and areolae on all 3 annuli between the oculars and the margin of the sucker, the annuli terminating on the ventrolateral margins of the sucker; vi, incomplete 4-annulate, $a_1=a_2 > (b_5+b_6)$ across the greater width of the dorsum, $a_2$ the 1st distinct annulus across the venter, forms the ventral margin of the sucker, $a_3$ the 2nd complete annulus (but see,

Fig. 1. *Abessebdella palmyrae* Richardson 1975. Lateral views showing annulation: A. anterior somites, B. posterior somites and sucker. C. Dorsal view showing general form and pattern.

Figures taken from the Holotype specimen, excepting Fig. 4. Somites and somital ganglia indicated by roman numerals; annuli, "$a_2$", etc.; somital limits, broken lines; somital ganglia shown at relative size. Scales, mm, 0.5 mm, or as indicated.

Abbreviations: a.g.m., ventral component of the anterior ganglionic mass; an., anus; at., atrium; con., dorsoventral connectives of the central nervous system; c.p., copulatory pore; dm.r., dorsomedian, and vl.r., ventrolateral internal muscular ridges of the pharynx; ej.b., ejaculatory bulb; f.p., female pore; i.r., inner ridge of margin of anterior sucker; int., intestine; j., jaw; l.o., lambertian organ; m.p., male pore; nepr., nephropore; nepr.p., nephroporic pit; o.r., outer rim of margin of anterior sucker; ov., ovary; ov.gl.s., oviducal glandular sac; p.c., postcaecum; p.g.m. posterior ganglionic mass; ph., pharynx; pr.l.m. procurrent, and re.l. recurrent limbs of the female median region; sp.d., sperm duct; spm., supramarginal somital sense organ; te., testis; v.d., vas deferens.


VIII
IX
VII
$b_5$
$b_6$
$b_1$
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$a_2$
VI
$b_5 + b_6$
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V
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IV
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nepr.
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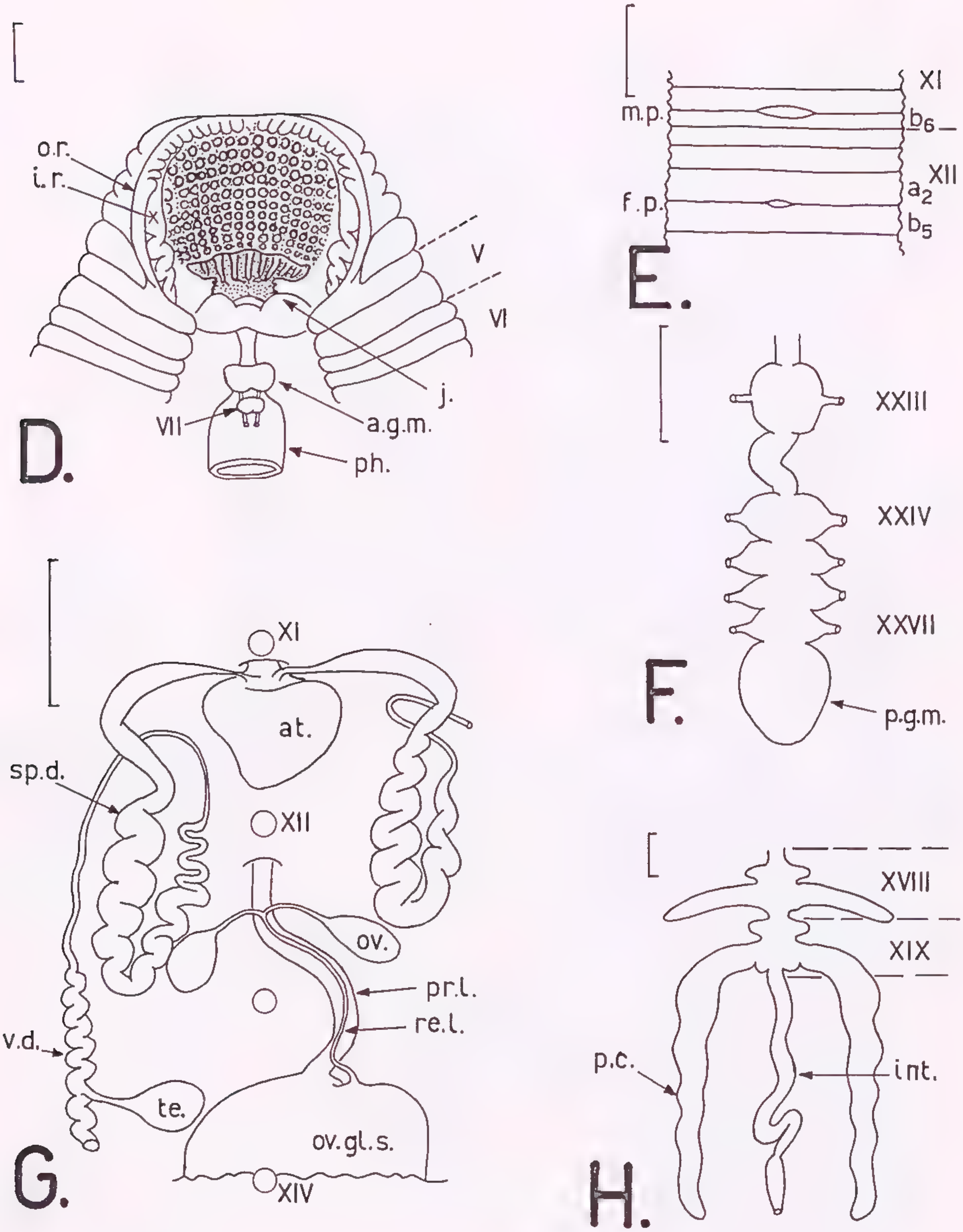

Fig. 2. *Abessebdella palmyrae* Richardson 1975. D. Anterior sucker, annular groove, jaws, anterior ganglionic mass, pharynx, etc., as displayed by a ventral median longitudinal incision. E. Ventral aspect, somites xi, xii, showing genital pores. F. Somital ganglia xxiii to xxvii and posterior ganglionic mass. H. Crop compartments xviii, xix, showing caecation, postcaeca, intestine. G. Anterior region of male paired ducts, male median region, the dorsal aspect of the atrium turned posteriorly, and female reproductive system. For abbreviations, etc., see Fig. 1.

Additional Material, 1); vii, complete 4-annulate $a_1 > a_2 > b_5 > b_6$, intermediate somital sense organs detectable on $a_2$; viii to xxiii complete 5-annulate (total, 16); viii, $b_1 < b_2 < a_2 > b_5 = b_6$, as also ix with the 2nd nephropores on $b_2$; x, xi, xii, $b_1 < b_2 < a_2 > b_5 > b_6$; xiii to xviii, $b_1 < b_2 < a_2 > b_5 = b_6$; xix to xxii, $b_1 = b_2 < a_2 > b_5 = b_6$; xxiii, $b_1$ slightly $< b_2 < a_2 > b_5$ much $> b_6$, the 16th nephropores on $b_2$; ?10+ "annuli" between xxiii $a_2$ and the anus; xxiv, incomplete 4-annulate, $b_1 < b_2 < a_2$ much $> a_3$, and below $(b_1 + b_2)$ the last annulus across the venter, $a_2$ and $a_3$ continue as thin ridges onto the dorsum of the sucker.

Somites xxiii and xxiv have erratic partial or complete transverse subdivision of some areolae.

The annulation of the incomplete somites posterior to xxiv is confused on the dorsum; the areolae large, papilliform to conical, jumbled without clearly indicated interannular furrows excepting a few immediately anterior to the anus.

The annulation can be assessed only as: xxv incomplete 3-annulate, $a_1 < a_2 = a_3$, $a_1 a_2$ in the margins; xxvi 3-annulate; xxvii apparently 2-annulate.

No defined auricles; interannular and intersomital furrows of xxv, xxvi, xxvii, continue to the lateral edges of the somites, as also the areolation.

A distinct nephroporic pit, acutely conical, the depth 2 or more times the width (0.2 mm) of the entrance which is situated beneath the ends of the contiguous annuli of xxv and xxvi. There is no papilla in the pit.

Dorsum of the posterior sucker with 4 concentric rows of areolae; the venter with a closely papillate central disc about 1/3rd of the width of the sucker, the outer papillae merging into about 56 radiating muscular ridges which divide to terminate as some 90 ridges at the margin; 9 muscular ridges extend into the clamp.

BODY WALL AND MUSCULAR SYSTEMS: The oblique muscular layers of the body wall are not obvious in dissection. The internal longitudinal layer is thick and formed of broad flat muscle strands in intimate contact and forming a distinct sheet.

The paramedian palisade of dorsoventral muscles is represented along the crop by clusters of strands at the intersomital levels. Posterior to xix, the mm. habenae (Richardson, 1977a.) are present as spaced, laterally compressed, heavy bands of muscles radiating from a restricted ventral base and more widely inserted on the dorsal body wall.

CENTRAL NERVOUS SYSTEM: Fig. 2D, F. The ventral component of the anterior ganglionic mass is situated in vi; ganglion vii, posterior in vi close to vi/vii, separated from the ventral component by less than ½ the length of ganglion vii.

Ganglion xxiii is the most posterior independent ganglion, separated by 1½ times its length from ganglion xxiv.

Ganglia xxiv, xxv, xxvi, xxvii, are a series of individual ganglia in intimate contact; xxiv, distinctly the larger; xxvii, in intimate contact with the posterior ganglionic mass.

ALIMENTARY TRACT: Fig. 2D, H. The dorsal, transverse margin of the anterior sucker is formed by an erect thin ridge-like primary fold, incised along the free edge to appear as though papillate or fimbriate. The fold divides in the lateral margins into a plain fold continuing to form the ventral margin, and a second fold internal and parallel to it on the lateral and ventral inner surfaces of the chamber of the sucker.

The internal dorsal surface of the chamber is coarsely and closely papillate.

The posterior face of the chamber is membranous, perforated by a wide transverse slit. The lateral and ventral portions of the membrane form the anterior wall of the well-formed annular groove which is deeper ventrally and laterally than dorsally. The dorsal surface of the groove is longitudinally plicate.

The jaws are housed in the annular groove. They are ventrolateral, transverse, subhorizontal; moderately compressed, minute, the medial end about 0.2 mm high and the width slightly less. The anterior margin is smoothly low convex, the length about 0.6 mm, and armed with a chitinous edge having the appearance of extremely minute teeth.

The entrance to the pharynx is a transverse slit about 0.3 mm wide; the dorsal margin, a thin fold forming a minute dorsomedian pad; the ventral margin, continuous with the bases of the jaws, slightly thickened and muscular, recognizable as a ventromedian muscular pad which is not attached to the wall of the annular groove.

Salivary glands were not recognisable in dissection.

The entrance to the pharynx leads into a short very narrow membranous-walled initial portion of the pharynx which passes through the circumpharyngeal elements of the central nervous system, widening in vii/viii into the pharynx proper. This is about 0.5 mm in diameter, very thin-walled; the internal surface, weakly rugose longitudinally and not divided into the usual primary ridges.

The pharynx terminates at a small sphincter at viii/ix.

The crop commences with a compartment in ix extended briefly laterally with a single pair of wide-based caeca. Each compartment in x to xviii carries a pair of short secondary caeca in the anterior position, and a longer pair of primary caeca in the posterior position, the primary caeca increasing in length to xiii, and then uniform in length, very narrow and elongate, almost tubular for the greater part of their length.

The compartment in xix has small secondary anterior caeca, and postcaeca originating at the posterior level, entering the paramedian splanchnic chambers to extend posteriorly and terminate in xxvi.

There are no lambertian organs.

The crop ends at xix/xx, connecting terminally to the narrowly tubular intestine, in turn connecting terminally to the short rectum.

REPRODUCTIVE SYSTEMS: Fig. 2E, G. Assessed as adult; female mature; male immature.

Genital pores xi $b_5/b_6$, xii $a_2/b_5$.

Testes saccular; 10 pairs located in the median chamber; the most posterior at xxii/xxiii; the anterior pair at xiii/xiv.

A vas efferens extends laterally from each testis, entering the paramedian splanchnic chamber to join the vas deferens which is compactly folded on itself and white to in xiii where it narrows into a thin-walled colourless duct. This duct turns medially in the vicinity of xi/xii to pass through the paramedian palisade of dorsoventral muscles and enter the median splanchnic chamber where it forms a posteriorly directed primary loop.

Both loops reflect in the contiguous halves of xii/xiii; the relationship, parallel. The recurrent and procurrent limbs of the loop are thin-walled, the duct progressively expanding on the recurrent limb to become a sperm duct which is closely folded along both limbs without differentiation as an epididymis.

The sperm ducts reduce abruptly in diameter in the vicinity of the male atrium, each connecting independently low on the anterior face of the atrium. There are no ejaculatory bulbs.

The male atrium is about 1.5 mm high, about 0.5 mm wide across the dorsal aspect and a little shorter than wide. It stands high above and conceals the ventral nerve cord and ganglion xi. The wall is thin, lacking developed layers of organised muscular tissues.

It is accordingly, mesomorphic and amyomeric.

The two saccular ovaries are in the contiguous annuli of xii and xiii, each continuing as a thin-walled transparent oviduct.

The oviducts join without a distinctive atrium and form the median region which is developed on a posteriorly directed primary loop reflecting at xiii/xiv.

The initial recurrent limb of the loop is a little wider than an oviduct, thin-walled, transparent, non-muscular, and less than half of the width of the thick-walled strongly muscular terminal procurrent limb which ends at the female pore. The two limbs are nearly equal in length.

The posterior face of the elbow of the loop is expanded posteriorly as the thin-walled glandular sac, terminating in xvii in the contracted specimen (possibly anterior to this in an extended specimen).

There is nothing recognisable as aggregated prostate or albumin glands.

PARATYPE: General form, colour (faded), pattern, as in the Type, but lacking indications of elongate oval dorsal patches.

General somital annulation as in the Type: v complete 3-annulate; vi, incomplete 4-annulate, $a_1=a_2$ $(b_5+b_6)$ above; vii, 4-annulate; viii to xxiii, 5-annulate with $a_2$ long, and 10 annuli between xxiii $a_2$ and the anus; areolae not jumbled on the posterior somites; nephroporic pit, as in the Type.

Genital pores, xi $b_5/b_6$; xii, $a_2/b_5$.

The primary fold on the margin of the anterior sucker dividing as in the Type; dorsal surface of the chamber of the sucker, papillate; entrance to the annular groove, the groove, entrance to pharynx, jaws, etc. as in the Type.

No obvious salivary glands.

Pharynx, crop, intestine, as in the Type.

No lambertian organs.

Reproductive systems as in the Type.

No aggregated prostate or albumin glands.

ADDITIONAL MATERIAL:

(1) B. P. Museum acc. 2083, Mitchill, June 13, 1935.

This contained the holotype, paratype, and 3 small specimens: (a) 5.5 mm long; (b) 5.2 mm long; (c) 5.75 mm long.

The three small specimens are similar in form, heavy-bodied: (a) 5.5 mm long is almost uniform in depth (1.0 mm) along the length of the body; the margins obtusely rounded, parallel from 1.5 to 4.5 mm from the anterior end with a width of 1.75 mm, narrowing very gradually anteriorly to 1.0 mm at v/vi; the posterior sucker, large, 1.7 mm long and 1.5 mm wide.

Colour, (a) and (b) uniformly darkish brown on all aspects as in juveniles, with white elevated obvious large rounded intermediate, supramarginal and submarginal somital sense organs; (c) the dorsum almost white with a very faint tinge of brown vaguely indicating two wide plain bands, and between these a median white stripe, margins and venter white as also both aspects of the posterior sucker, somital sense organs as in (a) and (b) but relatively smaller.

In all three, the eyes very large, protrudent, and each in a large ocular aerola.

General somital annulation, as Type in all three: v $a_2$ with obvious supramarginal and submarginal somital sense organs lateral to the ocular aerolae; 1st nephropores at iv/v lateral to the ocular areola; vi incomplete 4-annulate, $a_1=a_2<(b_5+b_6)$ above, $b_5/b_6$ very short and faint in (b), distinct in (a) and (c), and in all $a_1$ the 1st annulus complete across the venter; vii, $a_1>a_2>b_5>b_6$ in all; viii to xxiii 5-annulate, $a_2$ distinctly the longest annulus in all; 9 (? 10) annuli between xxiii $a_2$ and the anus, the count of a possible 10 annuli due to the presence on xxv or on xxvi of a weak short irregular broken furrow; xxiv, $b_1=b_2<a_2>a_3$ in all, and $a_1$ the last annulus complete across the venter; xxv 2-annulate; xxvi, xxvii, uniannulate. Posterior sucker as in Type.

In all three, xxv, xxvi, xxvii, swollen laterally as a low wide mound with a smooth lateral edge and not subdivided; a nephroporic pit beneath this mound.

The margin of the anterior sucker as in the Type in all three, and the dorsal surfaces of the chamber of the sucker, papillate.

Genital pores, xi $b_5/b_6$, xii $a_2/b_5$ in all three.

Specimens (a) and (b) have been retained with the Type in B. P. Museum acc. 2083. (c) has been deposited with the Paratype in the Australian Museum Coll, No. W. 7217.

(2) B. P. Museum No. 147. Palmyra Island. Collectors Thaanum and Thurston, No. 158.

One specimen, 22.0 mm long, in very poor condition, the surface epithelium eroded, the body soft, the wall fragile and broken.

Somite vi, $a_1<(b_3+b_4)<(b_5+b_6)$, although this is most unusual, the furrow $b_3/b_4$ is very definite, equivalent to $b_5/b_6$, and continues into the intermediate field; vii, $(b_1+b_2)<(b_3+b_4)>b_5>b_6$ below; viii, $(c_1+c_2)<(c_3+c_4)$ ? = $(b_3+b_4)>b_5<(c_{11}+c_{12})$ above, $a_1/a_2/b_5/b_6$ but distinctly $b_1/b_2/a_2/b_5/b_6$ below; ix to xxiii 5-annulate; 10 annuli between xxiii $a_2$ and the anus; 17th nephropores housed as in the Type.

Genital pores xi $b_5/b_6$, xii $a_2/b_5$.

No further information can be taken from the specimen.

### Genus **Elocobdella** Richardson 1975

1st nephropores labial, lateral to the ocular areolae of v; duognathous; no salivary gland papillae; vi incomplete 4-annulate, $(b_1+b_2)$ above, $a_1$ below; vii incomplete 5-annulate, $(b_5+b_6)$ above, $a_3$ below; viii and ix complete 6-annulate, $c_{11}$, $c_{12}$; x to xxiii incomplete 7-annulate, $(c_1+c_2)$, $b_2$, $a_2$, $b_5$, $c_{11}$, $c_{12}$, above and $b_1$ below; xxiv incomplete

5-annulate, $(b_1+b_2)$, $a_2$, $(b_5+b_6)$ above, $a_1$, $a_3$, below*; xxv incomplete 3-annulate; xxvi 2-annulate; 14 annuli on the dorsum between xxiii $a_2$ and the anus; no defined auricle; no nephroporic pit; lambertian organs, elongate, the duct very short; well formed ejaculatory bulbs; median regions of the reproductive systems, the male, an amyomeric, micromorphic atrium, the female with recurrent and procurrent limbs subequal in length; genital pores, xi $b_2/a_2$, xii $b_2/a_2$. Papuan. Australian Region.

Type Species: *Elocobdella novabritanniae* Richardson 1975. New Britain.

### **Elocobdella novabritanniae** Richardson 1975, p. 128.

Fig. 3.

Holotype: Total length, 16.0 mm. New Britain, Gazelle Peninsula, Mt. Sinewit, 5-14, xi, 1962. J. Sadlacek Collector. BISHOP. B.P.H. Museum Cat. No. 567. The Holotype, dissected, separated as Cat. No. 567A.

Paratype: Total length, 17.0 mm. Same location, date collector, as Holotype. Deposited Australian Museum, Sydney, Coll. No. W. 7216.

Additional Material: See below.

The paratype and additional material were referred to in the study of the holotype. The following description is taken from the holotype.

GENERAL FORM: Preserved, contracted, the annuli strongly compressed: dorsum transversely smooth high convex, the venter flat, and an abrupt transition between the dorsum and venter: depth uniform along the greater length of the body, as also the width with the greatest width along the posterior half of the body narrowing very gradually anteriorly and then abruptly close to the broadly obtuse anterior sucker; the posterior sucker slightly wider than its base.

Total length, 16.0 mm; at v/vi, 0.75 mm from the anterior end, the width 1.8 mm; at ix/x, 2.0 mm, the width 2.3 mm and depth 1.5 mm; at 4.0 mm, the width 2.5 mm and depth 1.8 mm, and essentially of these dimensions nearly to the anus at 13.5 mm; the posterior sucker, 2.8 mm wide and 3.0 mm long.

COLOUR: Preserved in alcohol. Off-white on all aspects as also the dorsum and venter of the posterior sucker, excepting for faded remnants of black bands on the dorsum of the body.

PATTERN: Preserved. Faded. On the dorsum in the middle of the body for a length of about three somites, indications of a narrow light contrast stripe filling the median field, defined by fragments of a pair of dark bands, each band including the line of the paramedian somital sense organs and extending into the paramedian field.

Lateral to and widely spaced from each band, an outer narrow paired dark band indicated along a length of some 15 somites by fragments along the line of the intermediate somital sense organs.

From these indications, the pattern includes a contrast stripe filling the median field along the greater length of the body; an inner and an outer pair of dark bands separated by a light stripe and the edges of the outer bands not sharply defined; venter, plain. See also Additional Material.

ANNULATION: Fig. 3 I, J, K. Preserved, contracted so that the annuli are strongly

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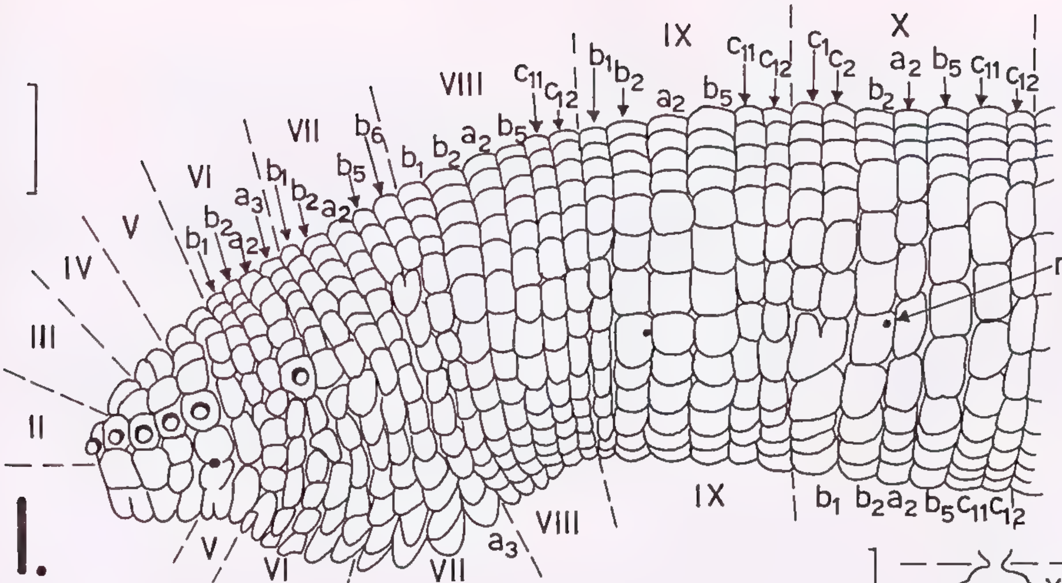
*The study of the additional material confirmed the annulation of xxiii and xxiv as above; not xxiv $(c_1+c_2)$, $b_2$, $a_2$, $a_3$, as originally recorded for the Type.

Fig. 3. *Elocobdella novabritanniae* Richardson 1975. Lateral views showing annulation: I., anterior somites, J. posterior somites (areolation omitted), and K., ventral aspect, somites xi, xii showing genital pores. L. Crop compartments xviii, xix, showing caecation, postcaeca, lambertian ducts and organs, intestine, rectum. M. Anterior region of male paired ducts, male median region, and female reproductive system. For abbreviations, etc., see Fig. 1.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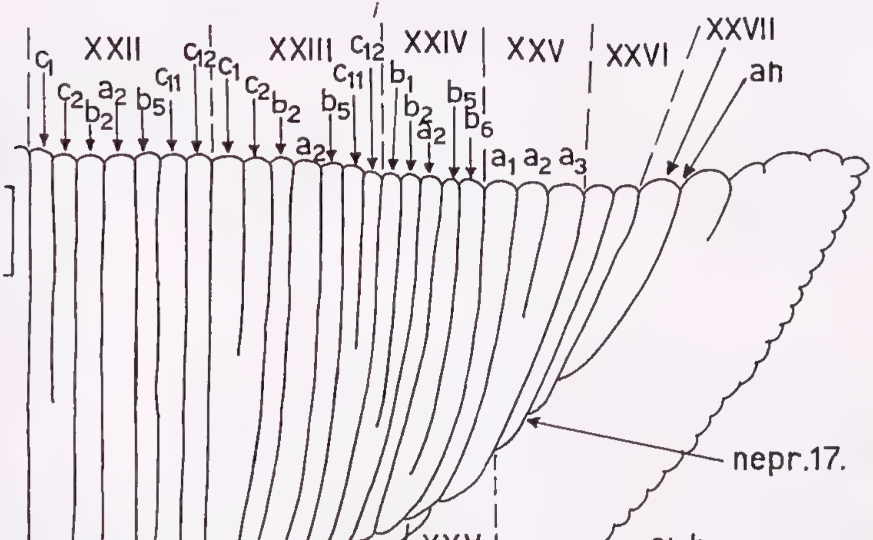
J.
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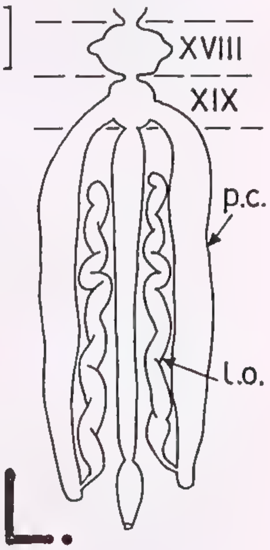
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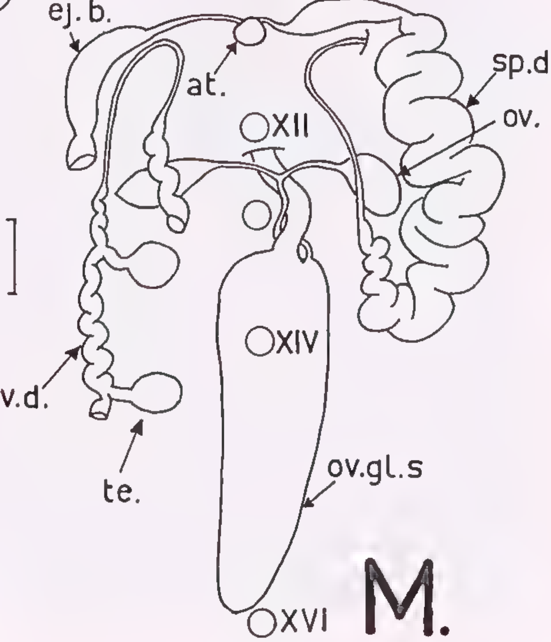
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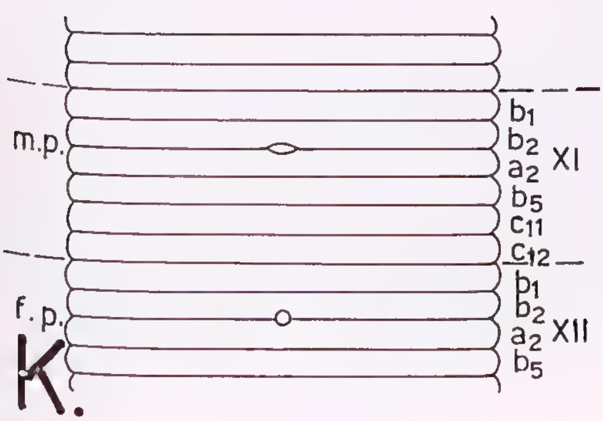
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XI
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b5
XII

compressed along the greater length of the body, and the areolae poorly defined excepting enlarged protrudent conical areolae on the ventral aspect of vi and vii; interannular and intersomital furrows deep, equivalent; somital limits not directly recognisable; somital sense organs generally obscure; nephropores, minute apertures on the posterior face of the nephroporic annuli, concealed and difficult to detect.

No defined preocular somite i between ii and the margin of the sucker; the eyes situated each in a distinct ocular areola, with areolae on ii to v lateral to the ocular areolae; ii uniannulate, the ocular areolae in contact; iii uniannulate, 3 areolae as a transverse row between the oculars; iv 2-annulate, $a_1a_2$ with 4 areolae $<$ $a_3$ with 4 areolae, $a_1a_2$ and $a_3$ joining to the ocular by a single common areola; v complete 2-annulate, $a_1a_2$ continues to the lateral margin of the sucker, $a_3$ along the ventrolateral margin; the 1st nephropores in v $a_1a_2$.

Somite vi is 4-annulate above, $(b_1+b_2) > a_2$ with the 5th eyes $> a_3$, the furrow $b_1/b_2$ short, terminating in the intermediate field, and $a_1$ below this.

There is difficulty in assessing with confidence the ventral annulation of vi where there are very large high conical papillae appearing in ventral view as though arranged in diagonal rows, and in lateral view $a_2$ dividing below the ocular areola into 3 annuli and $a_3$ continues across the venter.

Similar large papillae are present on the venter of vii, but vii is clearly incomplete 5-annulate, $b_1 < b_2 < a_2 < (b_5+b_6)$ on the dorsum, $b_5/b_6$ well defined across the median and paramedian fields, and $a_3$ below.

Somite viii and the following somites are strongly compressed; viii complete 6-annulate, $b_1 < b_2 > a_2 > b_5 > c_{11} = c_{12}$; ix 6-annulate, $b_1 < b_2 > a_2 < b_5 > c_{11} = c_{12}$, the second nephropores posterior on $b_2$.

Somites x to xxii, incomplete 7-annulate (total 13), ($c_1$ always much $<$ $c_2$), $(c_1+c_2)$ always much $>$ $b_2$, $c_1/c_2$ extends into the marginal fields, $b_1$ below this.

Somites x, xi, $(c_1+c_2) > b_2 > a_2 < b_5 < c_{11} > c_{12}$; xii to xx, the midnephric series, typically $(c_1+c_2) > b_2 < a_2 > b_5 = c_{11}, < c_{12}$, as also xxi, xxii, excepting $c_{11} = c_{12}$.

Somite xxiii and the following somites very strongly contracted, reduced in length, and difficult to assess on the lateral aspect. The annulation appears to be: xxiii, incomplete 7-annulate, $(c_1 + c_2) > b_2 < a_2 > b_5 < (c_{11} + c_{12})$ on the dorsum, with $c_{11} = c_{12}$, and $b_1, b_6$ below; xxiv incomplete 5-annulate, $(b_1+b_2) > a_2 < (b_5+b_6)$ above, $a_1/a_2/a_3$ below, and $a_2$ the last annulus fully formed across the venter; xxv, incomplete 3-annulate, $a_1 < a_2 = a_3$, $a_2/a_3$ terminating on the lateral aspect; xxvi 2-annulate, $a_1a_2, a_3$; xxvii uniannulate; 14 annuli on the dorsum between xxiii $a_2$ and the anus which is at the posterior margin of xxvii; an indication of a postanal annulus.

There is no formed auricle. The intersomital and interannular furrows of xxiv to xxvii, and the areolation continue to the lateral ends of all annuli and these do not coalesce. The 17th nephropores are beneath the lateral end of xxvi. There is no formed nephroporic pit.

The dorsum of the posterior sucker with some 4 concentric rows of areolae; the venter with a coarsely papillate disc about ½ the diameter of the sucker, and some 60 radiating muscular ridges.

CENTRAL NERVOUS SYSTEM: Ganglion vii is in close contact with the posterior face of the ventral component of the anterior ganglionic mass; ganglia xxiv, xxv, xxvi, xxvii, are in intimate contact, xxiv the larger, and xxvii in contact with the anterior face of the posterior ganglionic mass.

ALIMENTARY TRACT: Fig. 3, L. The anterior and lateral margins of the anterior sucker formed by a single papillate fold, dividing into an outer papillate fold completing the margin of the sucker, and an inner fold as a thick undulant ridge parallel to the outer fold; dorsal surface of the chamber of the sucker, closely and richly papillate, the papillae assembling into longitudinal rows continuing each as a ridge to the transverse slit-like entrance to the annular groove housing the ventrolateral jaws.

The jaws transverse, the anterior margin nearly straight, 0.5 mm long, the jaw 0.25 mm high at the medial end and strongly compressed; a low thin chitinous cutting edge appearing as though a row of closely crowded minute teeth, the row uniform in height along its length.

No detectable salivary gland papillae.

Entrance to the pharynx at vi/vii, a narrow transverse slit about 0.3 mm wide, the dorsomedian margin, a thin fold.

The pharynx is very thin-walled, narrowly tubular, the width posterior to the anterior ganglionic mass about 0.25 mm; the length about 0.5 mm; terminating at viii/ix.

The anterior end of the pharynx is firmly fastened to the body wall; the posterior portion, freely movable and extrinsic radial muscles are not obvious.

Salivary glands, not recognizable. No columns of aggregated ducts.

The thin-walled crop is strongly contracted; compartmented in xi to xviii, each compartment carrying a single pair of wide-based caeca centred on the middle of the compartment.

In xix, the compartment gives off a pair of postcaeca, each entering the paramedian splanchnic chamber and extending to the level of xxiv/xxv.

A very short lambertian duct commences subterminally on the ventral face of each postcaecum connecting to a lambertian organ which is elongate cylindrical, the width about 0.25 mm, closely applied to the ventral surface of the postcaecum, slightly convoluted to folded on itself, and extends into xx, so that the length even in this contracted specimen exceeds 3.0 mm.

The crop ends at xix/xx, connecting terminally to the narrow subcylindrical intestine which tapers before connecting terminally at xxiii/xxiv to the short simple rectum.

REPRODUCTIVE SYSTEMS: Fig. 3K, M. Adult, assessed as female, gravid. Contracted, the median regions closely compacted:

Genital pores xi $b_2/a_2$, xii $b_2/a_2$.

Testes, saccular, the posterior pair at xxii/xxiii, the anterior pair at xiii/xiv. A vas efferens extends laterally from each testis to join a white, compactly folded vas deferens extending anteriorly, reducing in width at xii/xiii to a narrow thin-walled delicate duct turning medially and entering the median splanchnic chamber in the posterior half of xi, extending posteriorly as a primary loop, the left reflecting in xv, the right in xiv, the two more parallel than tandem in relationship; no distinctly differentiated epididymis; a sperm duct on both limbs of the primary loop connecting to an elongate well-formed muscularized ejaculatory bulb; the bulb reducing to a narrow thin-walled ejaculatory duct; the ejaculatory ducts joining independently low on the anterior face of the minute thin-walled male atrium which is entirely ventral to the nerve cord, amyomeric and micromorphic.

The single pair of saccular ovaries are at xii/xiii; the thin-walled narrow oviducts join without an obvious atrium; the female median region formed on a posteriorly directed loop; the initial recurrent limb of the loop, thin-walled, narrow, much less than ½ of the width of the strongly muscular procurrent limb; the two limbs subequal, the recurrent only slightly shorter than the procurrent. The glandular sac extends into xvi.

Prostate glands, sparse, aggregated around the male atrium. There is no indication of aggregated albumin glands.

ADDITIONAL MATERIAL:

(1) The Type collection contained two other specimens, 14.0 mm, 8.5 mm, returned to the B.P.B. Museum as Cat. No. 567.

(2) One specimen, folded, 11.5 mm, same locality as the Type. BBM-N.G. 20781. 14. xi. 1962, ex Crake. H. Clissold.

(3) Noona Dan Expedition, 1961-62, Zool. Mus. København.
(a) Two specimens, 9.0 mm, 15.0 mm. On the path, Pathes-Yalom, 35 km. SE of Cape Lambert, New Britain. Ca. 600 m. 6-5-1962. 9.0 mm, faded, a pale median longitudinal stripe, fragments of a dark band along each side of this stripe; a pale stripe lateral to each dark band; fragments of a dark band lateral to each paired stripe; the whole indicating a dorsal pattern of 3 longitudinal light stripes and 4 longitudinal dark bands, the stripes and bands of nearly the same width.
(b) 1 specimen, 6.0 mm. On the ground, Rain Forest, Valoka, Cape Hoskins, New Britain, 13-7-62. Coll. T. Wolff. The median light stripe present along the posterior half of the body; wide undivided dark bands on either side of this stripe continuous laterally with a fragmented dark band. Pattern transitional between juvenile and adult.
(c) In nose cavity of young of *Casuarius*. Yalom, 35 km SE of Cape Lambert, New Britain, 1000 m. 12-5-1962. 4 specimens, 11.0 mm, 12.0 mm, 13.0 mm, 26.0 mm. Pattern, 11.0 mm, 12.0 mm, 26.0 mm, faded to spaced fragments of the dark lateral edges of the lateral bands. Nephropores commonly enclosed in small dark circles. The 13.0 mm specimen, a median longitudinal light stripe distinct from in iii to the anus; on each side of this in the 1/3rd quarter of the body, short lengths of pale dark bands, these lengths including a line of elongate pale ovals, each oval about half of the length of a somite; lateral to the dark band, a pale stripe narrower than the band, the lateral edge of each stripe continuous with triangular dark patches as a spaced row, the "apex" of each patch directed ventrally into a light stripe, dividing the stripe into suboval sections, the stripe paler than and distinct from the venter.
The pattern suggests these may be a second species.

### Gen. et sp? aff. g. **Barbronia** s.s. Johansson 1918.

Fig. 4.

The genus was based on *Barbronia rouxi* Johansson 1918, from Canala (= Kanala) New Caledonia. A specimen from Kanala, Australian Museum, Sydney, W. 1621, has been studied along with the following:

Eight specimens, B.P.B.M., No. R148. Palmyra Island. Thaanum & Thurston.

The description below is taken from a specimen 31.0 mm long. In this and others opened, the crop, intestine and testes are disintegrated and a complete description

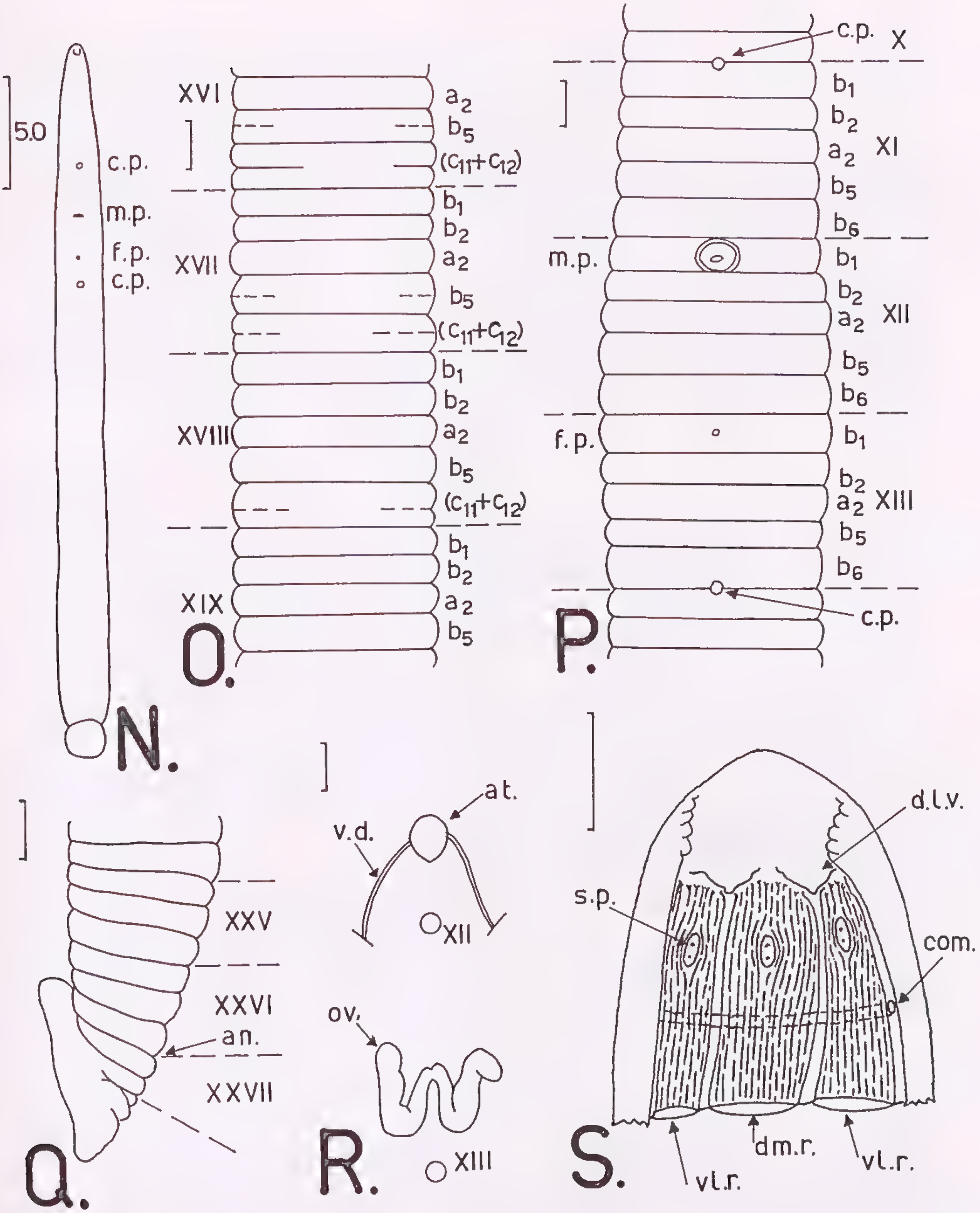

Fig. 4. Sp. aff. g. *Barbronia* s.s. Excepting O., the illustrations taken from the 31.0 mm specimen. N., Ventral aspect showing general form, the location of the genital pores and copulatory pores. Somital annulation; O., dorsal view, somites xvi to xix; P., ventral view, somites x to xiv, showing genital pores, copulatory pores; and Q., lateral view, somites xxv to xxvii and posterior sucker. R. Anterior region of male paired ducts, male median region, and female reproductive system. S. Chamber of the anterior sucker, entrance to and the initial portion of the pharynx, as exposed by a median ventral incision. For abbreviations, etc, see Fig. 1.

cannot be prepared.

GENERAL FORM: Fig. 4N. Elongate, subcylindrical, the width slightly greater than the depth; the dorsum and venter, very low convex; the margins obtusely rounded.

The anterior sucker, small, short, acute. The width and depth increasing very gradually to the clitellum which is not clearly indicated, uniform along the postclitellar region, the depth then increasing slightly in the posterior third of the body, and the width diminishing abruptly at the posterior end to form the base narrower than the circular sucker which is of the maximum width of the body. The anus is in advance of the base of the sucker which is continuous with the postanal portion of the body.

In the 31.0 mm specimen, the width at the posterior end of the anterior sucker is 1.0 mm, increasing to 2.0 mm and the depth 1.75 mm at x/xi, 5.0 mm from the anterior end, and of these dimensions posteriorly to 20.0 mm, the depth then diminishing to 1.5 mm, and of these dimensions to 27.0 mm, then diminishing to form the base of the sucker of which the ventral face is 2.0 mm long and wide.

COLOUR, PATTERN: Uniformly pale off-white; opaque; unpigmented; no indication of pattern.

ANNULATION: Fig. 4 O, P, Q. Extended, curved ventrally longitudinally so that the dorsal annulation is weakly defined to obscure; intersomital and interannular furrows, equivalent, generally detectable with difficulty on the dorsum and venter, or entirely lacking, faintly to more definite on the lateral aspects. The annulation is not complete in any specimen; no couplets or triplets of annuli; no obvious dermal papillae, nephropores, somital sense organs; eyes, not detectable.

The following somital annulation is assembled from several specimens. As is usual in these leeches, the posterior annulus in most somites is distinctly long, longer than the anterior annulus of the following somite. The posterior annulus, $b_6$, is commonly recognizable in fully divided somites as subdivided on the dorsolateral aspects into $(c_{11}+c_{12})$, with $c_{11} > c_{12}$, the furrow $c_{11}/c_{12}$ occasionally recognisable on the dorsum but not on the venter. In some specimens (Fig. 4.0.) $b_5$ appears very weakly divided on the margins, but this is irregular and not recognised below.

In one specimen, there are 2 annuli, ii, iii, anterior to uniannulate iv which forms the lateral and ventral margins of the sucker; v, incomplete 2-annulate, $a_1a_2 < a_3$ above, uniannulate below; vi, 3-annulate; vii, ?; viii 4-annulate in 2 specimens, $a_1=a_2 < b_5=b_6$; ix to xi appear to be 5-annulate; ix $b_1 > b_2 < a_2=b_5 < b_6$; x, $b_1 < b_2 < a_2=b_5 < b_6$; xi, $b_1 > b_2 < a_2=b_5 < b_6$. Somites xii to xxii incomplete 6-annulate; xii $b_1 > b_2 < a_2 < b_5=(c_{11}+c_{12})$, as also xiii.

In the middle series in one specimen, in the vicinity of xvi to xviii, 3 somites have $b_1 > b_2 < a_2 < b_5 < (c_{11}+c_{12}), > b_1$, with $c_{11} > c_{12}$.

Somite xxiii, $b_1 > b_2 < a_2 < b_5 < b_6$; xxiv, 4-annulate, $b_1=b_2 > a_2 < a_3, >$ xxv $a_1$; xxv, 3-annulate, $a_1 > a_2 < a_3, >$ xxvi $a_1$; xxvi, 3-annulate, $a_1 < a_2 > a_3$, $a_2$ the last annulus formed across the venter; xxvii, 2− (possibly 3−) annulate; 2 accessory postanal annuli; anus, xxvi/xxvii.

Obvious large copulatory pores, x/xi, xiii/xiv; genital pores, xii $b_1$, xiii $b_1$; male pore everted in some as a low conical non-muscular penis, as is typical of the amyomeric micromorphic male atrium; female pore, a minute aperture.

ALIMENTARY TRACT: Fig. 4,S. The chamber of the anterior sucker, small, short, the dorsal margin of the sucker papillate in one specimen (as also A.M.W. 1621), smooth in two others; lateral and ventral margins, papillate or smooth. There is nothing in the nature of a well-defined annular groove.

Posterior in the chamber of the sucker, a right and a left dorsal valve, triangular in form, the base anterior, the valves extending posteriorly each as a free flap with the apex entering the anterior end of the dorsolateral groove between the dorsomedian and ventrolateral primary internal muscular ridges of the pharynx. A.M.W. 1621, lacks flaps but has a papilla at the anterior end of each of these grooves.

The entrance to the pharynx is anterior to the dorsoventral connectives of the central nervous system, and between the entrance and the connectives is a wide chamber with the anterior ends of the primary muscular ridges in the dorsomedian and ventrolateral positions, and median in each, a small smooth style pocket with two minute stylets in tandem, the stylets lacking in one or two pockets in some, and one specimen lacking pockets on the ventrolateral ridges.

Posterior to the dorsoventral connectives, the dorsomedian ridge narrows on the left, expands on the right, and in this way the dorsomedian ridge is transposed into the right ventrolateral position.

This is correlated with a narrowing of the margin along the dorsal edge of the right ventrolateral and expansion of the ventral edge of this ridge medially, transposing the ridge into the ventromedian position.

The left ventrolateral ridge continues unchanged in position to the end of the pharynx which terminates in xiii.*

The crop, intestine and rectum are decomposed with nothing remaining of these structures (as also in A.M.W. 1621).

REPRODUCTIVE SYSTEMS: Fig. 4P,R. Testes, not recognizable. The vasa deferentia obvious in xii as very narrow delicate white ducts extending anteromedially to connect independently to the thin-walled male atrium which is small, about 3 times the length of a somital ganglion, and entirely ventral to the nerve cord in xii $b_1$.

Ovaries, tubular, short, folded and entirely in the anterior half of xiii, each connecting to the bursa which is minute and does not rise above the body wall.

There is no indication of aggregated prostate or albumin glands.

## SYSTEMATIC STATUS OF THE PALMYRA BARBRONID.

This requires review of the knowledge of barbronids.

Barbronids are aquatic strepsilaematous macrophages; eyes in transverse pairs, a dorsal anterior and two lateral pairs; 14 pairs of ventral nephropores; pharynx, terminating in xiii, with or lacking stylets; anus, xxvi/xxvii; genital pores, anterior in xii

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*Oka (1923. *Annot. Zool. Japan.* 10:243-252) in distinguishing between the euthylaematous and strepsilaematous forms of pharynx, described the change in position of the primary internal muscular ridges in the strepsilaematous pharynx as resulting from torsion. It has been referred to in this way since then. Opening the strepsilaematous pharynx by a longitudinal incision commencing at a ventral corner of the margin of the sucker, the right corner in those I have examined including erpobdellids, shows the dorsomedian and one ventrolateral transposing as described here, with the other ventrolateral unchanged in position as described also by Moore (1927) in *Herpobdelloidea lateroculata* and *H. indica.* Accordingly the term ‘torsion’ is not appropriate.

and xiii; median copulatory pores, x/xi, xiii/xiv; so far as known, a small number of saccular testes, 5 to 12 pairs irregularly arranged, some in clusters, in xiii, xiv, to xvi; anterior region of male paired ducts, tubular, linear, joining to the male atrium; ovaries, tubular connecting directly to the female bursa; cocoon, where known, with a plain translucent thin wall, depressed oval, a plug at each end, attached by the flat lower surface to stones and other objects.

Johansson (1918) forecasted a family (Barbronidae), but took no action. The barbronids became assigned to the Erpobdellidae s.l., and on the presence of stylets associated with such leeches as the ethiopian *Salifa perspicax* Blanchard 1897, the oriental *Herpobdelloidea lateroculata* Kaburaki 1921, v. Soós, 1970; the ethiopian *S. elongata* Moore 1931; and the oriental *Nematobdella indica* Kaburaki 1921 (v. Soos, 1966a,b).

Barbronids resemble erpobdellids in general facies; ocular pattern; general somital annulation; nephropores; the nature of the pharynx, crop, female system; and where known, the cocoon. The resemblances are similar to those shared by the different families of aquatic jawed sanguivores, and not familial in status.

They differ from typical erpobdellids in having stylets; the genital pores anterior in xii, xiii, not xi, xii; median copulatory pores at x/xi, xiii/xiv, not known in erpobdellids; a small number of saccular testes in xiii, xiv to xvi, not multiple testes in xiii, xiv, and posteriorly into xxii, or further.

Barbronids differ from the *Salifa* group which lacks copulatory pores and has multiple testes in xiii, xiv, to xxiii, xxiv, or with a few in xiii and posteriorly into xxiii, or xvii to xxiii (Moore, 1927, 1939, 1958). In these features, as in some others, the *Salifa* group is more erpobdellid than barbronid. *S. elongata* is exceptional in having the pharynx extending to xv.

The barbronids s.s. divide into:

(A) The male median region, a micromorphic amyomeric atrium; somites of the middle series 5– or incomplete 6– annulate with $c_{11}+c_{12}$ above, $b_6$ below: gg. *Barbronia* s.s., New Caledonia, *Vivabdella,* both Richardson 1971,? *Dineta* Goddard 1909, Eastern Australia; the Palmyra barbronid; as also others known to me in New Guinea, Tasmania; and New Zealand (Mason, 1976)*. *"Dina" weberi* Blanchard 1897, Java, is 6-annulate with $c_{11}$,$c_{12}$ complete, and might belong to this group.

(B) The male median region, a mesomorphic atrium with cornua; somites of the middle series 7-annulate, $b_1$, $b_2$, $b_3$, $b_4$, $b_5$, $c_{11}$, $c_{12}$, or further subdivided.
g.*Sciobdella* Richardson 1971, based on *"Barbronia weberi"* as in Moore (1927), India, also *"B". weberi* var. *formosana* as in Moore (1946) based on *Herpobdella formosana* Oka 1927, Formosa, and others in Amoy, China, Manchuria, and the Hawaiian Islands. Moore (1946) refers to the male pore as in xi $b_1$, $b_1/b_2$, a possible lapsus.

The Palmyra barbronid differs from the original description of *B.rouxi* and from the specimen A.M.W. 1621: ii, iii, iv, uniannulate — *rouxi,* ii, iii, 2-annulate, iv 3-annulate (possibly incomplete 4-annulate), 1621, ii and iv 2-annulate; v, incomplete 2-annulate — *rouxi* and 1621, 3-annulate; viii, 4-annulate — *rouxi,* 6-annulate, 1621 incomplete 5-annulate; ix to xi, 5-annulate — *rouxi,* 6-annulate, 1621, incomplete 7-annulate with $c_1/c_2$, $c_3/c_4$ very weak as noted also by Johansson.

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*Mason assigns the New Zealand specimens to *Barbronia weberi* (Blanchard, 1897) as in Moore (1927). This cannot be sustained.

The three are in agreement in the incomplete 6-annulate nature of the somites of the middle series and in the location of the genital pores and copulatory pits.

## ACKNOWLEDGEMENTS

I am grateful to the Director and to Dr D. M. Devaney, Invertebrate Zoologist, of the Bernice P. Bishop Museum, Honolulu, as also to Dr Torben Wolff of the Universitetets Zoologiske Museum, København, and to the Director, to Miss E. Pope and Dr P. Hutchings, the Australian Museum, Sydney, for the opportunity to study the leeches reported on in this paper.

I have been assisted with literature by the Librarians, CSIRO, the University of New England, and the Australian Museum. Professor Emeritus Marvin C. Meyer, University of Maine, has been most helpful with difficult literature.

This study has been greatly facilitated by the scholarly accounts of the genera and species in the Hirudinea, published by Dr A. Soos, the Hungarian Natural History Museum.

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Manuscript accepted for publication 27 March, 1980.

# REVISION OF THE TALBRAGAR FISH BED FLORA (JURASSIC) OF NEW SOUTH WALES

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## SUMMARY

The three well known form-species of the Talbragar Fish Bed Flora—*Podozamites lanceolatus, Elatocladus planus* and *Taeniopteris spatulata* — are redescribed as *Agathis jurassica* sp. nov., *Rissikia talbragarensis* sp. nov. and *Pentoxylon australica* sp. nov. respectively. The minor components of the assemblage are described and illustrated, and in some cases, reclassified. Additions are made to the list of plants recorded from the horizon.

## INTRODUCTION

The Talbragar Fish Beds are characterised by their beautifully preserved fish and plant remains which occur in great profusion throughout the shale lens which comprises the Beds. The ochre-coloured shale is ferruginous, with impressions of plants and fish, white in colour, standing out dramatically. The weathering of the outer layers of blocks of the shale has resulted in contrasting bands of iron-rich stain framing many of the specimens and enhancing their appearance. Specimens are much prized by collectors.

The fossil locality is the valley of the Talbragar River, about twenty miles due North of Home Rule Mine in the Cassilis District, "on the southern boundary of Boyce's selection" (Anderson 1889). Foldvary (1979) describes the locality as the northern slopes of Farrs Hill, North East of Gulgong.

The Talbragar Fish Beds are considered to be Early to Middle Jurassic in age (Hind and Helby, 1969 in Geology of New South Wales). Dr P. R. Evans of the University of New South Wales kindly undertook a palynological examination of samples submitted by the author, but was unfortunately not able to obtain any diagnostic spores.

The Fish Beds were discovered by Mr A. Lowe of Wilbertree in 1889. The Geological Surveyor of the New South Wales Mines Department, Mr William Anderson, described his visit to the site in that year (Anderson 1889) and remarked on the very large numbers of specimens which were awaiting transportation. These specimens, obtained from the splitting up of the oblong or square blocks of shale "which lay scattered over the surface of the hill", and not from excavating the underlying beds of the hill, are the Cullen Collection. The many thousand specimens of this first collection are held by the Mining Museum, Sydney, and until recently were stored in their original crates at the Mines Department Depot at Londonderry. The contents of the crates had been superficially examined once (one crate by Mining Museum staff and three by The Australian Museum), since the specimens were packed away in 1890. At the time of their crating, they had been briefly examined by Mr W. S. Dun, Assistant Palaeontologist (a cadet at the time) and by Mr R. Etheridge Jr., the Government Palaeontologist. A selection of specimens, representing all the fish species present, was sent to Mr A. Smith Woodward at the British Museum, and resulted in his monograph on the fish (Woodward, 1895). A small number

Records of The Australian Museum, 1981, **Vol. 33 No. 15,** 695-721, Figures 1-53.

of specimens containing all the plant species were also selected, and a plant list was published by Etheridge in 1889. Walkom, 1921, wrote his account of the Talbragar flora from a study of these specimens.

As a result of the first brief inspection of the specimens at Londonberry in 1978 by Dr A. Ritchie, Dr R. Molnar and the author at the start of this revision, a request was made for further study of the collection. Dr J. Pickett, Principal Research Officer of the Mining Museum, kindly arranged for the specimens to be brought back to Sydney and supplied facilities for their examination. The collection is now housed at the Mining Museum and two hundred of the best plant specimens have been registered.

When the (approximately) five thousand specimens of the Cullen Collection were closely examined, a count was made to show the relative proportions of the components of the flora. (The specimens reported on by Walkom were added into the tally.) As *"Podozamites lanceolatus"* occurs as foliage spurs of several leaves and a twiglet, an occurrence of the species was recorded for each twiglet or recognisable fragment of such. Single leaves were not recorded. For *"Taeniopteris spatulata"* the unit was single leaves or reasonable sized fragments of leaves. All recognisable fragments of other components of the flora were recorded.

On this somewhat arbitrary basis, there were 1300 occurrences of *"Podozamites"* and 1060 of *"Taeniopteris"*. The relative rarity of *"Elatocladus"* with only 75 occurrences was surprising. (The Museum collections of The Australian Museum and the Mining Museum had been made by selecting specimens to show the different components of the flora from collections other than the Cullen. The impression thus gained was that *"Elatocladus"* was second in dominance to *"Podozamites"*, instead of a relatively rare member of the flora.) Pteridosperm leaves of the *Pachypteris crassa* and *"Thinnfeldia pinnata"* type together numbered 300 occurrences. Fifteen conifer fragments of *Allocladus milneanus* type and only 9 of the *Allocladus cribbii (Brachyphyllum)* type, show the rarity of the lesser conifers in the assemblage. There were 27 occurrences of *Coniopteris hymenophylloides* (mostly small fragments) and only ten of *Cladophlebis australis*. Only one frond of *Nilssonia compta* was found, and one specimen with branchlets of a *Selaginella*.

The reproductive structures found were six large *Agathis ("Podozamites")* cone scales, five young *Agathis* cones and two pollen cones — a total of thirteen structures relating to the 1300 occurrences of *"Podozamites"*. There were six *Pentoxylon* female cones *(Carnoconites)* and two groups of microsporangia presumably of *Pentoxylon*, making eight structures relating to the 1060 occurrences of *"Taenopteris"*. There was one cone fragment (and counterpart) of the *Rissikia* type relating to the 75 occurrences of *"Elatocladus"*, and one group of detached seeds of the sort borne by *Rissikia talbragarensis*.

In all the specimens examined, there was no fragment which could be indentified as of insect origin, and the only insect found to date in the Talbragar Fish Beds is *"Cicada lowei* Etheridge" which was found in a specimen from the Cullen Collection in 1890 (Etheridge and Olliff, 1890).

From this analysis of the relative proportions of the species comprising the vegetation at Talbragar in Jurassic times, a clear picture emerges, of a lake containing many fish in an area of "Kauri Pine" forest. Numerous smaller trees of *Pentoxylon* grew interspersed in the forest (in much the same way as *Banksia* trees today form a lower tree zone below eucalypts) with occasional scattered trees of *"Elatocladus"* and podocarpaceous conifers, and with a heath zone surrounding the lake composed of

*Pachypteris* type Pteridosperms. A few ferns and rare cycads grew in suitable places in the forest and the lake surrounds. *"Cicada lowei"* presumably stridulated loudly in the trees at certain seasons.

## GENERAL DISCUSSION OF THE TALBRAGAR FISH BED FLORA

### 1. "**Podozamites lanceolatus** L. & H."

The dominant plant is *"Podozamites lanceolatus"*, the name used by Dun and retained by Etheridge in 1889. Walkom (1921) continued the use of this name when he wrote the first detailed account of the Talbragar Flora. It is most unfortunate that this name was ever used, as it was not acceptable. The specimens described and illustrated by Lindley and Hutton (1836) from the Jurassic of Great Britain as *Podozamites lanceolatus* are superficially similar to the Talbragar material, but Lindley and Hutton's species was a cycad as the name implied, and it is quite clear from their descriptions and illustrations that the pinnae were arranged in two ranks in cycad fashion, attached to the sides or possibly the top of the rachis. The Talbragar specimens clearly show a spiral phyllotaxy of leaves, not pinnae, and the characteristic branchlets with numerous leaves of different sizes are obviously foliage spurs which abscissed readily from the plant. They are clearly not pinnate cycad fronds. Dun and Etheridge should have referred the specimens to the conifer genus *Albertia* which had been described by Schimper in 1874 in a treatise available to them at the time, or to another conifer genus.

When Walkom reviewed the plants in 1921, he would have had Seward's (1900) revision of *Podozamites lanceolatus* available to him, and should have been aware that the attachment of the pinnae and their arrangement was stressed, indicating cycad affinity. Walkom did recognise that the Talbragar Specimens were most probably conifer foliage, and he should have corrected the mistake and renamed them accordingly. Florin (1940) in his review of Southern conifers, suggested that *"Podozamites lanceolatus"* in the Australian Jurassic was probably podocarpaceous. Townrow's (1967 a, b) revision of conifers, including some Talbragar species, does not touch on *Podozamites.*

Present day limited usage of *Podozamites* Braun 1843 as a form genus for detached conifer foliage, in which the leaves look like individual pinnae of *Zamites,* continues. In Laurasia, cones are known in association with leaves of this sort, which are invariably detached; never in foliage spur arrangement. The cones are *Cycadocarpidium* and *Swedenborgia* type. In South Africa, Anderson (1978) has just described a new cone *Telemachus* associated with leaves of *"Phoenicopsis elongatus* (Morris) Seward 1903", which is now referred to *Podozamites elongatus.* Thus it is no more appropriate to classify the Talbragar specimens in *Podozamites* as it is now defined, than it was to place them in *Podozamites lanceolatus* originally.

A review of living conifers and some study of specimens in the National Herbarium and of trees growing in the Royal Botanic Gardens, Sydney, was undertaken as a preliminary to revising the Talbragar gymnosperms. Although in leaf shape there are podocarpaceous genera which resemble *"Podozamites lanceolatus"*, all are characterised by a prominent midrib. It is with *Agathis* that the greatest affinity exists.

The Talbragar material not only shows a full range of leaf size and form all consistent with *Agathis,* but the deciduous foliage spurs are also diagnostic of the genus, and the only reproductive structures which can be related to the foliage are young female cones of Araucarian type (*Agathis* is Araucarian) and cone scales undeniably of *Agathis.* Prior to this investigation, Walkom (1921) had described a "young Araucarian cone" (his Fig. 6, Plate 6), and several more have now been discovered. *Agathis* trees growing in the

Botanic Gardens in Sydney have numerous aborted female cones in the litter of foliage spurs beneath them, and only a few mature cone scales are interspersed. (See Figure 20 A, B.) Only relatively few female cones reach maturity and these explode into component scales on impact with the ground when knocked down as they are borne at considerable heights, or they shed the scales gradually while still attached to the tree.

The first mature cone scale found in the Talbragar Fish Beds was described by Walkom (1921) as *Araucarites grandis*. Although obviously Araucarian, it differs from the other relatively common type found in this investigation and recognised as belonging with the *Agathis* foliage. At this stage of knowledge, it is considered to be a varietal form. (As the *"Elatocladus planus"* foliage and the lesser conifers of the assemblage are regarded as podocarpaceous, its affinities are also almost certainly with the *Agathis* foliage.)

*"Podozamites lanceolatus* L. & H." is redescribed as *Agathis jurassica* sp. nov. It is not possible to call it *Agathis lanceolatus* as there is a living species with that name.

### 2. "**Elatocladus planus** (Feist.)"

Conifer foliage with long, linear leaves with prominent midribs, attached spirally, was referred to the form species *Elatocladus planus*. Walkom (1921) states "these plants form a large proportion of the Talbragar collections" as he was not aware of how much selection had been done in the assembling of the small collection of representative plants. In his review, Townrow (1967b) retained the Talbragar specimens in the form species because he had no additional evidence of cuticle structure or related fructifications, other than the fragmentary "? Cone fragments" which he mentions (p.121). He stated, however, that there was some overlap with his genus *Rissikia* and that several true species might be represented by the *"Elatocladus planus"* he re-defined.

The discovery of a magnificent cone (Figure 26) in a specimen recently bought by the Museum from a private collection has enabled the determination of *Elatocladus planus* foliage as a podocarpaceous conifer. There are foliage leaves attached to the base of the cone, so the relationship of cone and leaves is positively identified. It was the acquisition of this cone which prompted the examination of all available specimens from Talbragar to look for fragmental evidence related to it, as it is a perfect, virtually complete specimen, and there had never been any suggestion of such a fructification by seeds, scales or fragments. Only one cone fragment and one specimen with loose seeds were discovered in this investigation.

The cone is an elongated, cylindrical structure made up of units each composed of a bract with a scale in its axil, and a reflexed ovule borne on the scale. Thus in essence it is of the same general structure as *Rissikia* (Townrow 1967b). The bracts are prominent and leafy, unlike the reduced, trifid structures in *Rissikia*. Bearing in mind the amount of variation in structures of cones which is tolerated within a genus of living conifers like *Podocarpus* (see Bucholtz and Gray 1948 and Gray, 1953), it is considered preferable at this stage to describe the Talbragar cone as a new species of *Rissikia* and not to create another new genus. No firm conclusions can be reached on whether all the foliage types are one species.

The name *Rissikia talbragarensis* sp. nov. is given to the cone and the attached leaves, and to some part (still undefined) of the *"Elatocladus planus"* form species foliage associated with it in the Talbragar Fish Beds fossil horizon.

### 3. "**Taeniopteris spatulata** McClelland"

The second commonest foliage in the Fish Beds is long, narrow, taeniopteroid leaves which are referable to the form species *Taeniopteris spatulata.*

Walkom (1921, Figs. 4, 4a, 7; Plate 6) illustrated as "?cones", two of the very rare examples of casts of cone-like bodies. The specimen in his Figs. 4, 4a unfortunately cannot be found at the Mining Museum. The one which is illustrated in Walkom's Figure 7 was cleaned and a latex mould was made from it. The result was a perfect fructification, which is illustrated in Figure 37 of this paper. A slender axis bears a number of sessile, ridged seeds in four alternating whorls of five. This is a *Carnoconites* type fructification (Srivastava 1946), and its discovery is very exciting as it enables the determination of the leaves of *Taeniopteris spatulata* and the fruit as *Pentoxylon.* Two further examples of fructifications of this sort were found during this investigation, and a new species *Pentoxylon australica* is made.

The Pentoxylaceae were described from the Jurassic Rajmahal Series in India. (Sahni, 1948; Vishnu-Mittre 1958; Pant, 1957). *Pentoxylon* silicified wood, *Taeniopteris spatulata* type leaves and *Carnoconites* cones were shown to belong together. In 1962, Harris described a new species of *Carnoconites* from New Zealand, also with *Taeniopteris spatulata* type leaves, so the discovery of *Pentoxylon* in Australia has been expected.

Wood of *Pentoxylon* type occurs in Australia. A silicified stem was recently acquired by The Australian Museum and it appeared to be of this type. It was sent to Dr. R. Gould at Armidale University for further study and he (pers. comm.) confirms that it is of the same sort as that described from India.

Thus, the three best known form species of the Talbragar Fish Bed Flora, *"Podozamites lanceolatus"*, *"Elatocladus planus"*, and *"Taeniopteris spatulata"* are all assigned to their appropriate botanical classifications on factual information, and are removed from the form genera to which they had originally been referred.

Detailed examination of so much material in connection with the revision of the three species has resulted in elucidation of new facts about lesser components of the flora. Walkom's *"Brachyphyllum"* conifer, which was redescribed by Townrow as *Allocladus cribbii,* is shown to be podocarpaceous. His *"Pagiophyllum peregrinum"* was identified by Townrow as *Allocladus milneanus.* No attempt has been made in this revision to deal with the Pteridosperms as they were revised by Townrow (1965). Some additions are made to the list of species identified by Walkom, and a complete new list of the flora and fauna of the Fish Beds is given below:

### SPECIES COMPRISING THE FLORA OF THE TALBRAGAR FISH BEDS

1. *Agathis jurassica* sp. nov. Foliage *"Podozamites lanceolatus* L. & H." Young female cones, mature cone scales, male pollen cones. Araucariaceae.
2. *Rissikia talbragarensis* sp. nov. Foliage, female cone. Podocarpaceae. Foliage of *"Elatocladus planus"* form species type.
3. *Pentoxylon australica* sp. nov. Foliage, female fructifications, groups of male microsporangia. Leaves of *"Taeniopteris spatulata"* form species type. Pentoxylaceae.
4. *Allocladus cribbii* Townrow. Foliage and cones. Podocarpaceae.

5. *Allocladus milneanus* (Ten. Woods). Townrow. Foliage. Podocarpaceae.
6. *Elatocladus australis* (Freng.) Foliage. Podocarpaceae.
7. *Nilssonia compta* (Phill.) Harris. Nilssoniaceae. (Cycadales).
8. *Selaginella* sp. Selaginellaceae (Lycopodiales).
9. *Onychiopsis* sp. Fern fragment.
10. *Cladophlebis australis* (Morr.) Fern fragments.
11. *Coniopteris hymenophylloides* Bgt. Fern fronds. Dicksoniaceae.
12. *Pachypteris crassa* Townrow. Pteridosperm fronds.
13. "*Thinnfeldia pinnata* Walkom (pars.)" Pteridosperm or fern fronds.

## FAUNA OF THE TALBRAGAR FISH BEDS

Insecta: *Cicada lowei* Etheridge & Olliff 1890.
Fish: (Sherbon Hills, 1958)
*Coccolepis australis* Smith Woodward
*Uarbryichthys latus* Wade
*Aetheolepis mirabilis* Smith Woodward
*Aphnelepis australis* Smith Woodward
*Archaeomene tenuis* Smith Woodward
*Madariscus robustus* Smith Woodward
*Leptolepis talbragarensis* Smith Woodward

## PALAEOBOTANY

### 1. **Agathis jurassica** sp. nov.

Figures 1-15

Classification: (Arnold 1948)
Gymnospermophyta.
Class. Coniferophyta
Order. Coniferales
Family. Araucariaceae
Genus. *Agathis*. Salisbury 1807
*Agathis jurassica* sp. nov.

Foliage:
"*Podozamites lanceolatus* L. & H."
Specimens AMF 59990, MMF 23682, AMF 59983
Female Cones:
*Agathis* cone scales. Specimens MMF 24075, 24123, 24076, 24074, 24077.
Scale in Fig. 13 lent by Mr R. Moffitt, private collection.
Immature female cones. AMF 59984, MMF 23943, 24080, 24135, 24079.
Male Cones:
Small, fragile pollen cones. MMF 24082, 24081.
Mature Female Cone Scale:
"Araucarites grandis" Walkom 1921. MMF 3170 = *Agathis jurassica var grandis* (Walkom) nov. comb.

a. Foliage

Leaves lanceolate, when mature between 4 and 7 cm long, maximum width between 0.5 and 0.75 cm, arranged in lax spiral on foliage spur branchlets with 20-40 leaves. Each leaf has 5-8 parallel veins.

The range of leaf form seen in the species is illustrated in Figures 1-4. The common forms are Figures 1, 2, 4 with wider leaves, but narrower types are part of a series and do not seem to represent a separate species. In counting occurrences of the foliage in the Cullen Collection, a note was kept of the narrowest leaves which are of *"Podozamites gracilis"* type (Fig. 3) and might represent a separate species. Only 14 of this sort were recorded. There may well be two varieties of the species, the one with consistently wider foliage which ranges to fairly narrow, and the other with *"gracilis"* foliage ranging into medium-wide. In view of the variation in cone scale type found, one considerably longer than wide (var. *grandis* (Walkom)), and the other ovate, there is some added suggestion that this may be so.

The very pronounced foliage spur nature of the branchlets makes their original inclusion in a species with cycad affinity the more surprising. Figures 2 and 4 show the swollen stem bases with scale leaves. Whether the spurs were shed annually as in the extant *Metasequoia,* or at longer intervals as in *Podocarpus imbricata,* another living conifer with deciduous spurs, is not known. The leaf spur arrangement with swollen stem bases is a feature of *Rissikia* (Townrow 1967b) and is also seen in *"Elatocladus planus"* from Talbragar, though as a less obvious character. The living species of *Agathis* growing in the Royal Botanic Gardens, Sydney, has a ground cover of shed spurs below them representing some of that year's new growth. They do not have swollen stem bases, and the bud scales from the overwintering bud remain loosely round the stem bases as the new shoot grows out through them in the spring.

### b. Female Cones

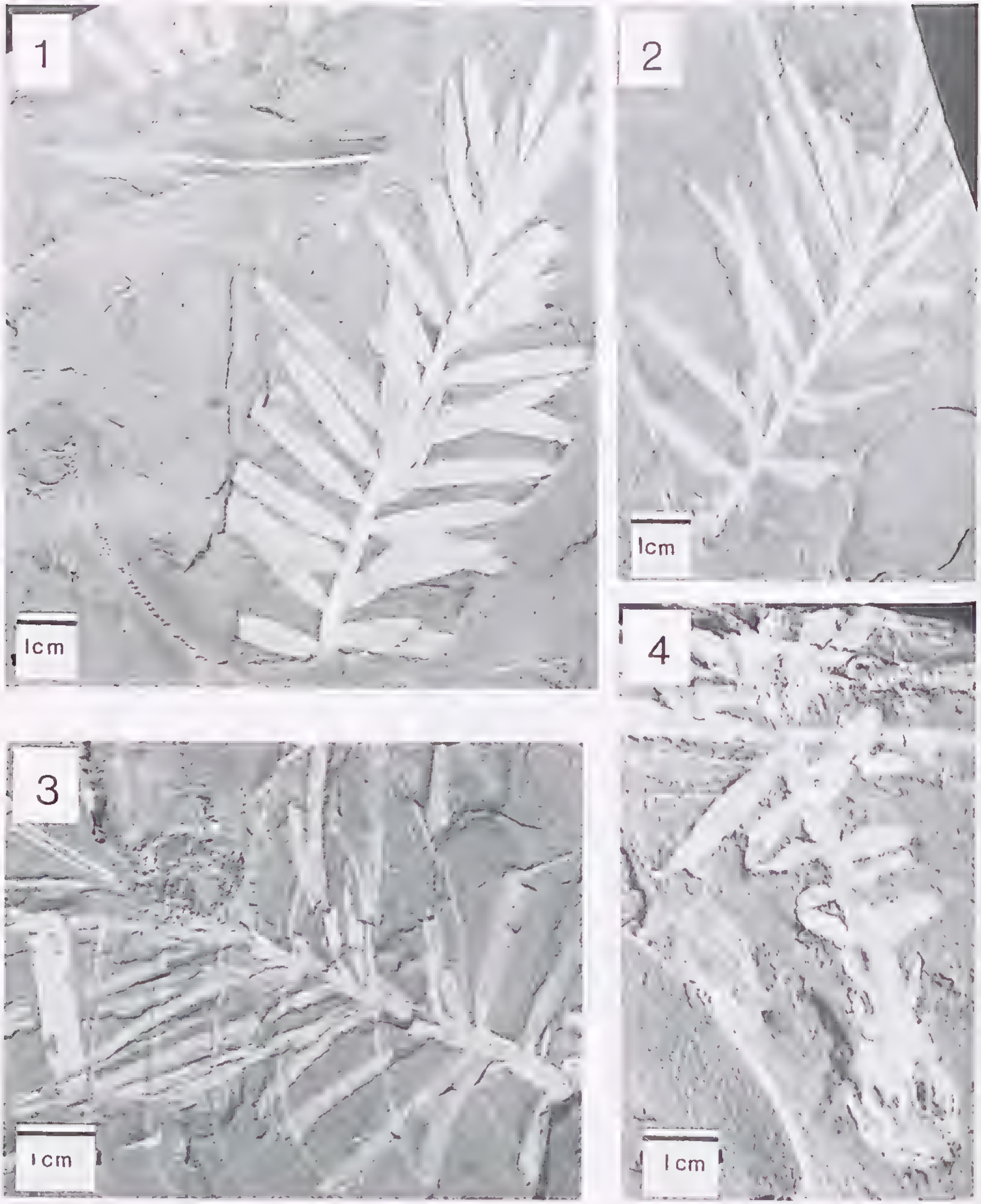
Walkom (1921, Fig. 8, Pl. 6) illustrated a young Araucarian cone. The specimen has been lost, but a similar one was found in The Australian Museum collection (AMF 59984, Fig. 7), and others were found in the Cullen Collection. (Specimens MMF 23943, 24080, 24079, 24135.) The cones are cylindrical, at least twice as long as they are wide. (Compare these cones with aborted cones of *Agathis robusta,* Figure 20 A,B.)

Walkom's mature cone scale *"Araucarites grandis"* has been cleaned, and is re-illustrated in Figure 5 (MMF 3170). It differs from the others found in this investigation in its proportions, being relatively long and narrow with a wide, wrinkled area between the seed indentation and the apical point of the scale. The other scales are much broader in proportion to their length, the apical point is less marked and, because they are relatively common, they are assumed to be the typical scales of *Agathis jurassica* and are so named (Fig. 6,10,11,13). Walkom's *"grandis"* type is retained as a variety — *Agathis jurassica* var. *grandis* (Walkom) nov. comb., applied only to the scales at this stage of knowledge.

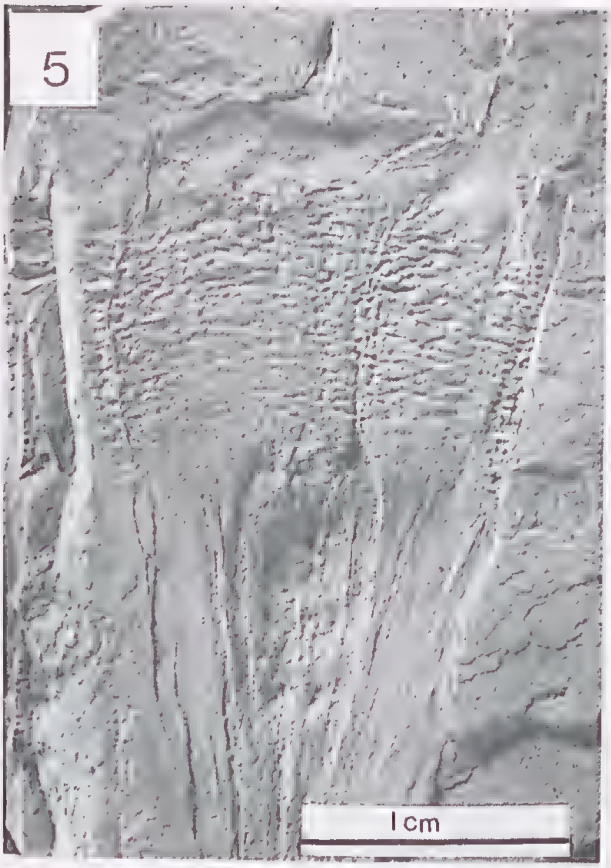
### c. Male Cones

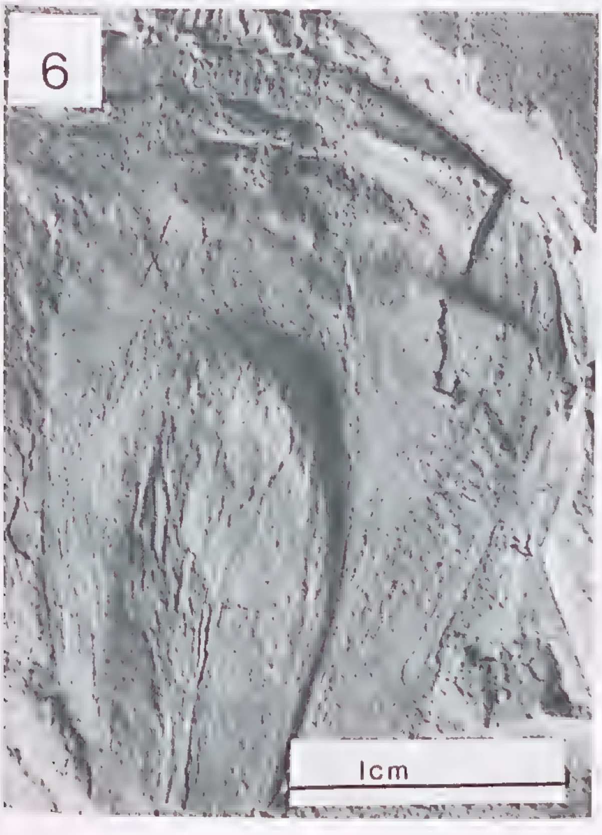
Two very delicate organs, believed to be male cones, are present on specimens MMF 24081 and 24082. Figure 9 illustrates one of them. They are poorly preserved but are obviously cones, and their delicate, papery texture is what would have been expected. There are also two examples of very small spherical cones found in the Cullen Collection. One is illustrated in Figure 8. They may be very young female cones, or could be male, and their affinities are not known.

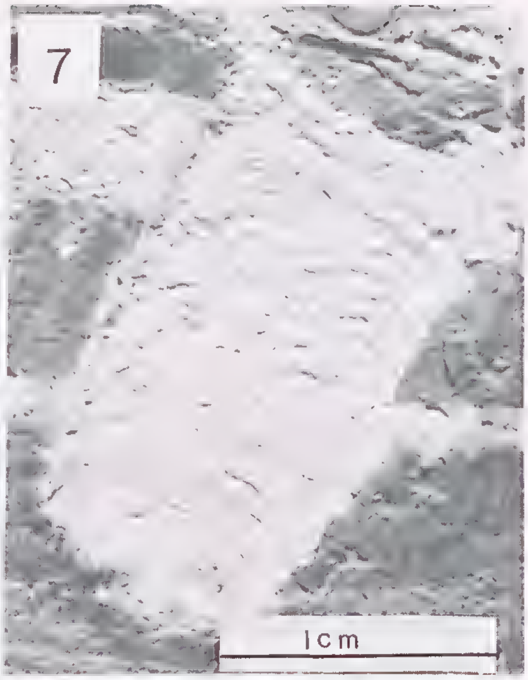
A living *Agathis (A. robusta)* is illustrated in Figure 20 to show the foliage, the appearance of leafy branchlets, young and mature female cones, and cone scale and pollen cone.

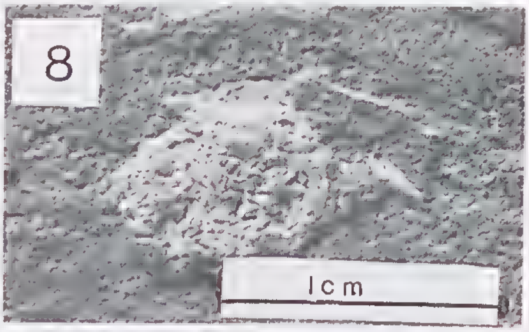


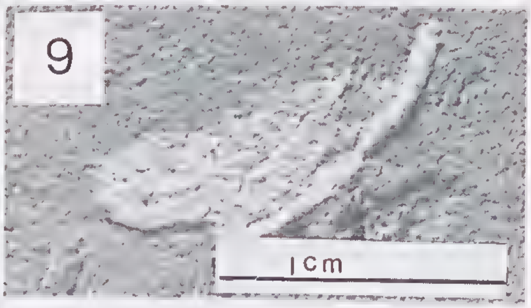
Figures 1-4. *Agathis jurassica* sp. nov. Figs. 1 & 2. Foliage spurs. AMF 59990. ½ natural size. Fig. 3. *"gracilis type"* foliage. MMF 23682. Natural size. Fig. 4. Foliage spur. Enlarged stem base with scale leaves. AMF 59983. Natural size.











Figures 5-9. *Agathis jurassica* sp. nov. Fig. 5. "*Araucarites grandis* Walkom" MMF 3170. X3 = *Agathis jurassica* var. *grandis* (Walkom). Fig. 6. Cone scale. MMF 24075. X3. Fig. 7. Young cone. AMF 59984. X3. Fig. 8. Small cone. MMF 24073. X3. Fig. 9. Pollen cone. MMF 24082. X3.

The distribution of *Agathis* in the modern world is significant as it is a genus of Southern Hemisphere origin, extending marginally into the Northern Hemisphere in relatively recent times (Bucholtz 1948). "Kauri Pines" today occur in two areas in Queensland and otherwise are confined to the eastern Pacific, extending from the Philippines to New Zealand and from Malaysia to Fiji. In the Tertiary, a conifer referred to *Dammara* by Ettinghausen (1888) and now recognised as *Agathis* (Florin 1940) occurred throughout eastern Australia from north Queensland to Tasmania. Cone scales associated with *Dammara* leaves are clearly referable to *Agathis*. Figures 16-19 illustrate leaves and a cone scale of *Dammara intermedia* from the Vegetable Creek mine at Elsmore, N.S.W. These specimens were illustrated by Ettinghausen (1888, pl. 8, Figs. 34,35,36,38).

### 2. **Rissikia talbragarensis** sp. nov.

Figures 21 - 31

Classification: (Arnold 1948)
Gymnospermophyta.
Class. Coniferophyta
Order. Coniferales
Family. Podocarpaceae
Genus. *Rissikia* Townrow 1967
*Rissikia talbragarensis* sp. nov.

Foliage:
"*Elatocladus planus* (Feist) Townrow". Specimens MMF 23689, MMF 17857, AMF 38839, AMF 58289, AMF 59992.
Female Cone:
*Rissikia talbragarensis* sp. nov. AMF 59822, MMF 23946.
Seeds:
MMF 3151.

a. Foliage

The range of leaf form seen in the Talbragar material is shown in Figures 21 - 25. Complete foliage spurs are seen in Figures 21 and 25. Townrow retained the full range in *Elatocladus planus* but there may be more than one species involved.

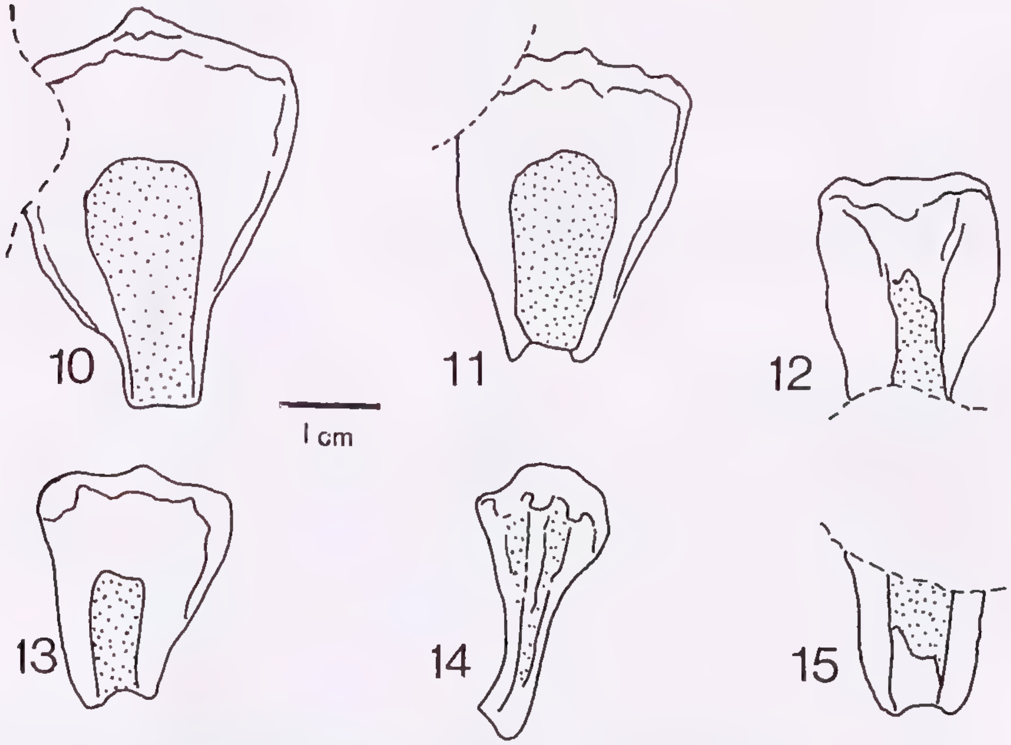
b. Seed Cone

The cone in Figures 26,27,28 has foliage leaves attached to it (L in Fig. 27), so that there is no doubt that the linear leaves with prominent midribs, which are indistinguishable from individual leaves of *Elatocladus planus*, belong to the cone.

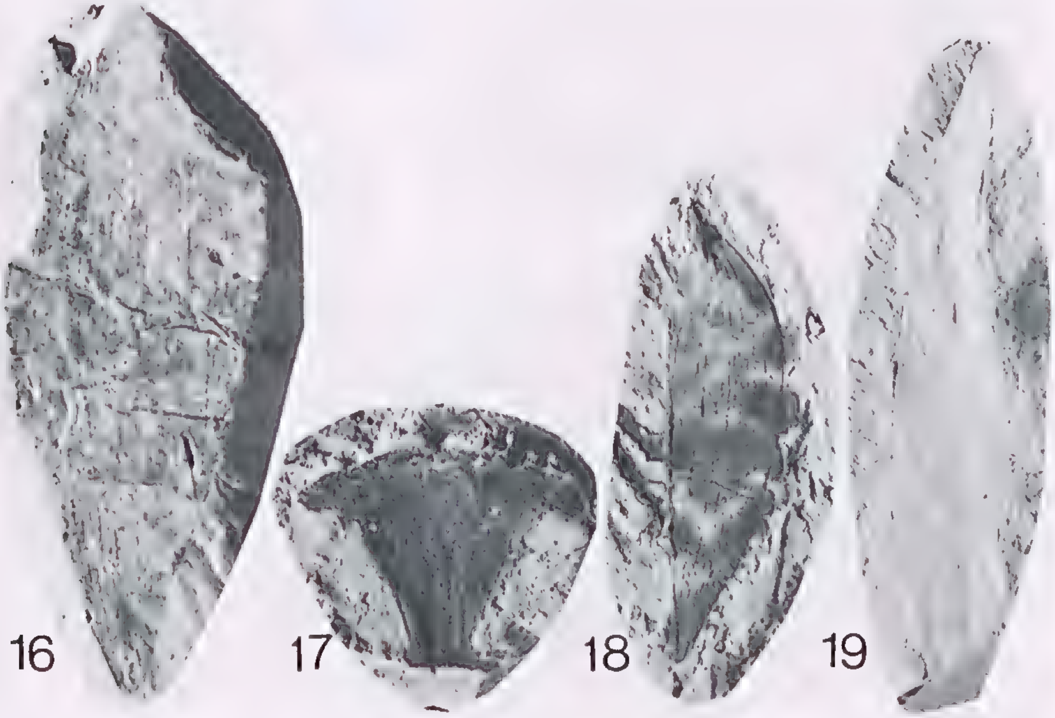
The cone is 12 cm long from its lowest seeds to its bluntly rounded apex. It has a stem 5.5 cm long and 0.4 cm wide from which two linear leaves arise at approximately 2 cm intervals. The maximum width of the cone is 2 cm. It tapers to 1 cm at its base, and approximately 1.5 cm at its apex. There are about thirty whorls of seeds, each measuring 3 mm by 2 mm, oval and reflexed with their micropyles towards the cone axis. The bracts are leafy with bluntly rounded apices. Preservation is not perfect and they may be lobed with the central part prominent and two lesser lobes flanking it.

A fragment of a cone found on specimen MMF 23946 (counterpart MMF 24134) is illustrated in Figure 29. It shows that the seed is borne on a scale. The scale is in turn borne in the axil of the leafy bract (Fig. 30).

Figure 31 shows specimen MMF 3151 in which loose seeds are present, of the type seen in the *Rissikia talbragarensis* cone.



Figures 10-15. Tracings of *Agathis jurassica* cone scales. Fig. 10. MMF 24075. Fig. 11. 24123. Fig. 12. MMF 24076. Fig. 13. R. Moffitt specimen. Fig. 14. MMF 24074. Fig. 15. MMF 24077.



Figures 16-19. *Dammara intermedia* Ettinghausen. Fig. 16. AMF 51216. Natural size. Fig. 17. AMF 51150. Natural size. Fig. 18. AMF 51139. Natural size. Fig. 19. AMF 51171. Natural size.

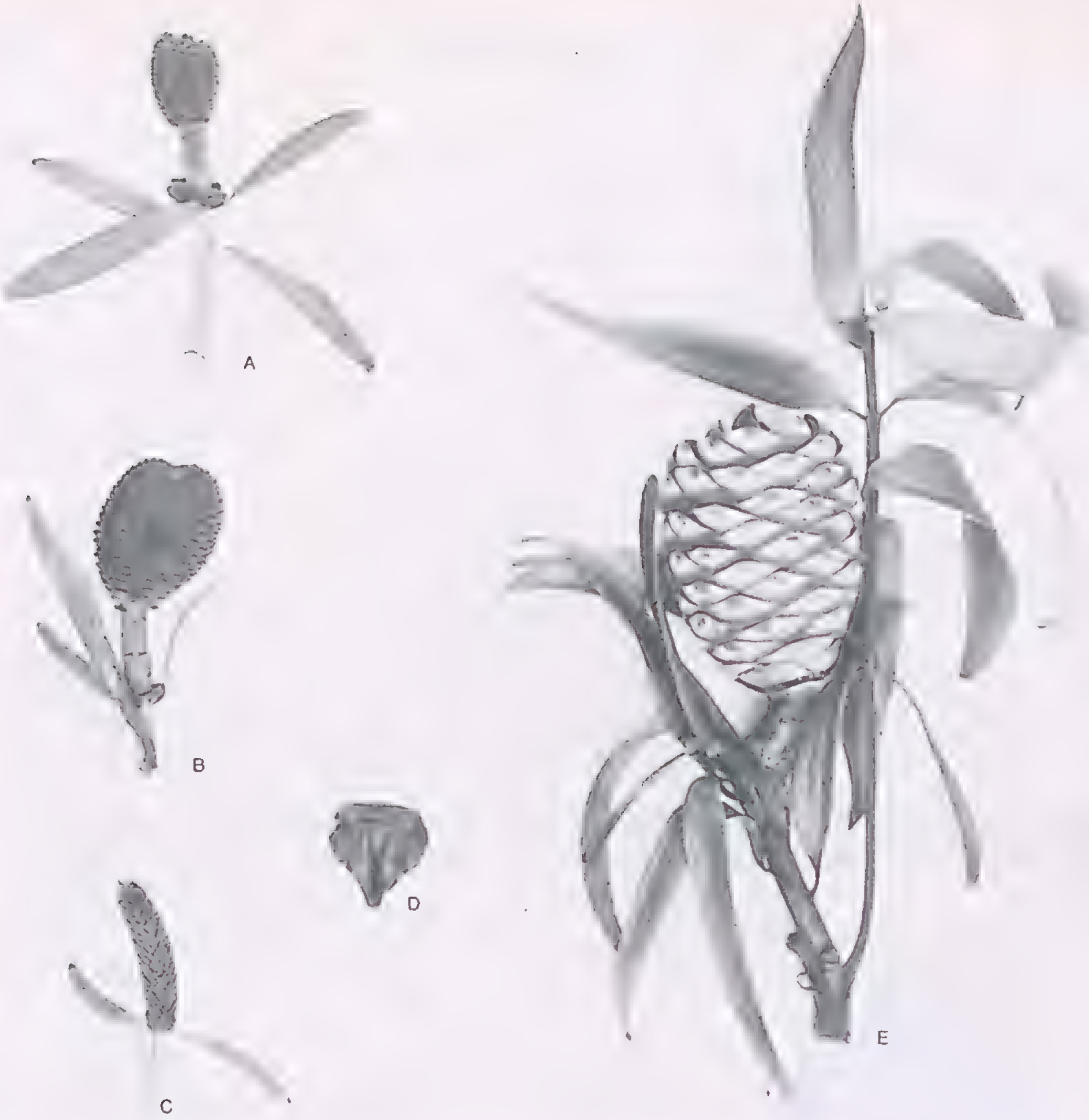


Figure. 20. A modern *Agathis (A.robusta)* to show foliage and cones. *A, B,* young female cones. *C,* pollen cone, *D,* female cone scale *E,* foliage and mature female cone.

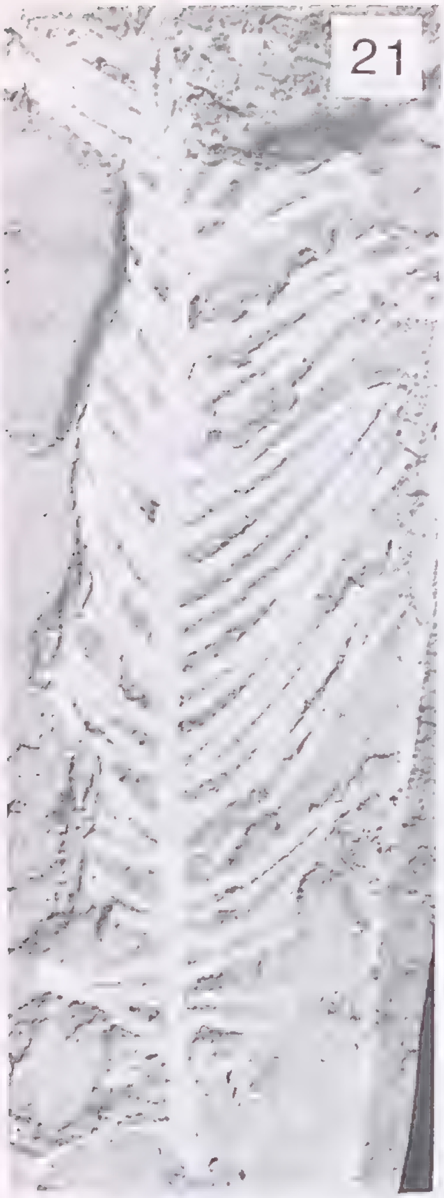
### 3. **Pentoxylon australica** sp. nov.

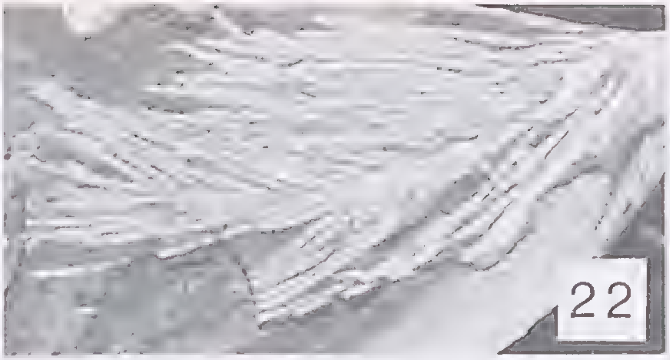
Figures 32 - 43

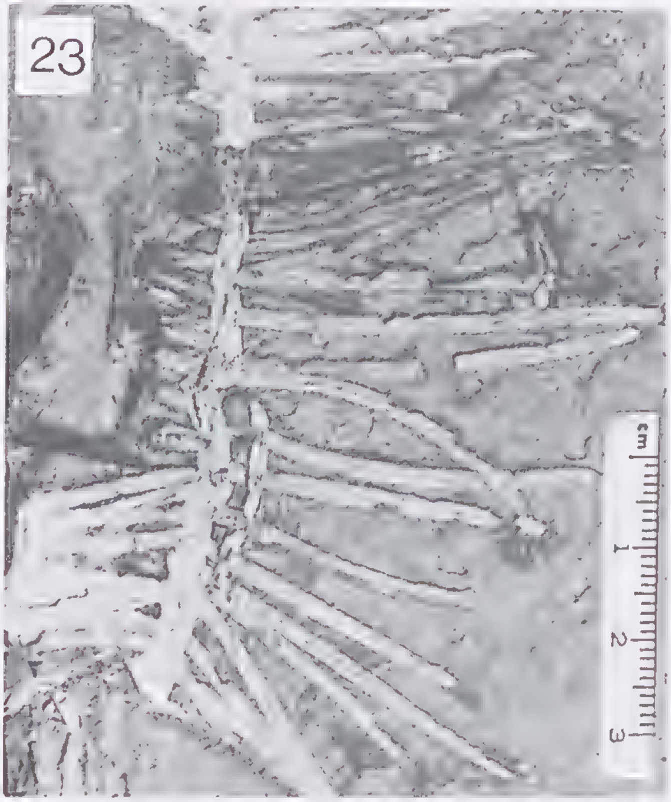
Classification: (Pant 1957)
Division. Cycadophyta
Class. Pentoxylopsida
Order. Pentoxylales
*Pentoxylon australica* sp. nov.

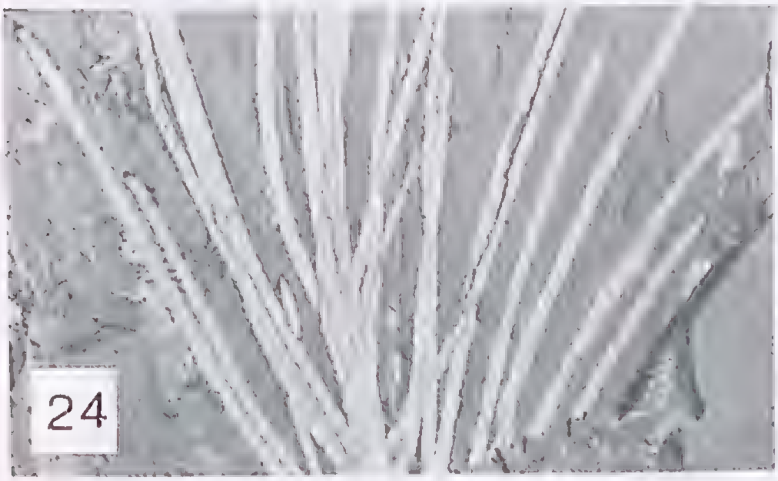
Leaves:

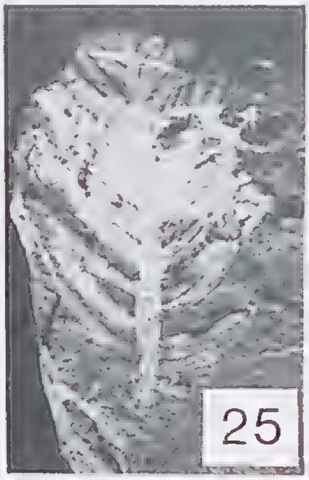
*Taeniopteris spatulata* McClelland. Known from impressions only. Specimens AMF 38831, 58454, 59994, 16443.











Figures 21-25. *Rissikia talbragarensis* sp. nov. foliage. Fig. 21. MMF 23689. Natural size. Fig. 22. AMF 38839. Natural size. Fig. 23. AMF 58289. Natural size. Fig. 24. MMF 17857. Natural size. Fig. 25. AMF 59992. Natural size.

26

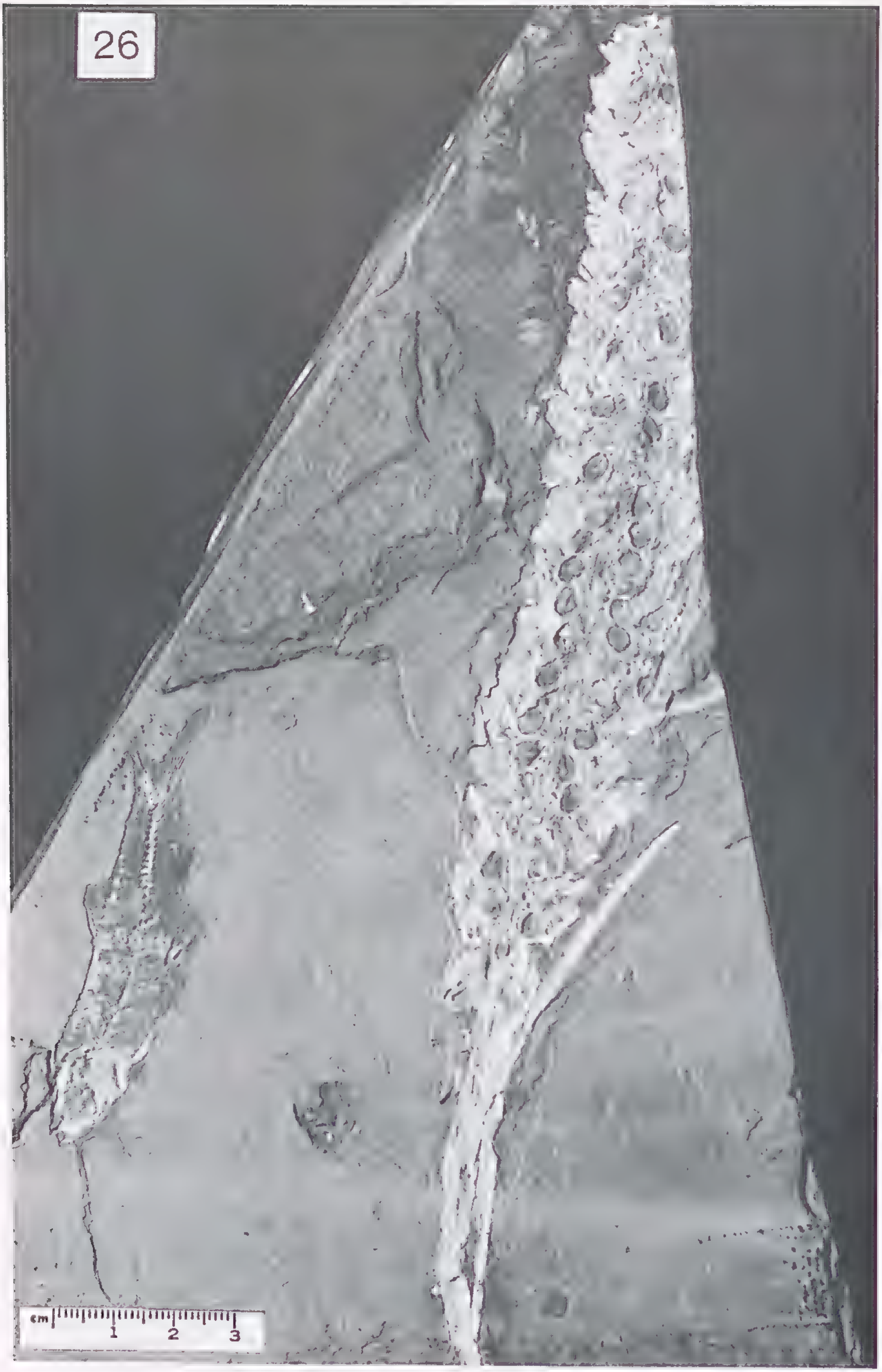
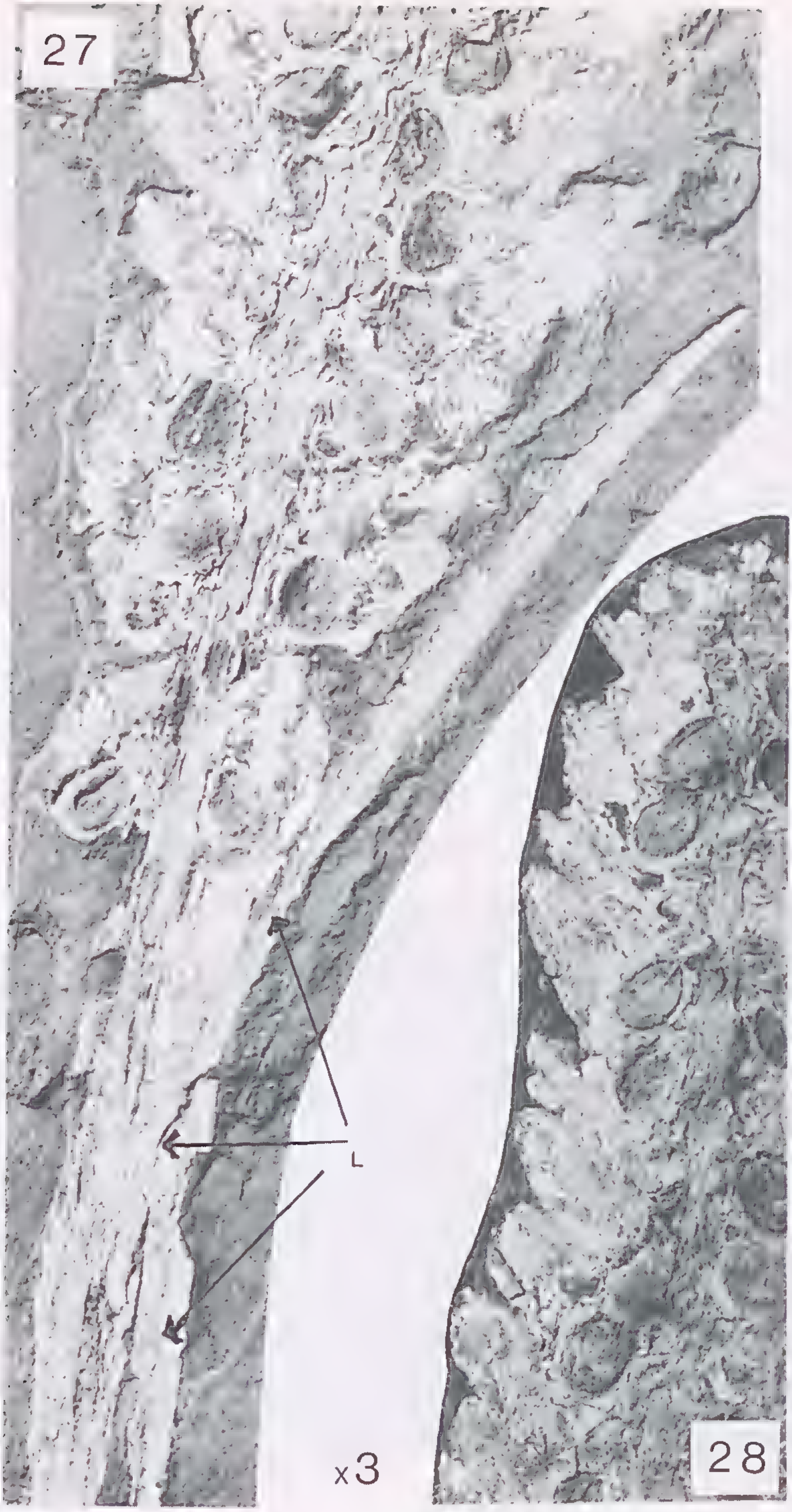


Figure 26. *Rissika talbragarensis* sp. nov. Seed Cone. AMF 59822. Natural size.



Figures 27 & 28. *Rissikia talbragarensis* sp. nov. Fig. 27. Base of cone, AMF 59822. Magn. X3. Foliage leaves at L. Fig. 28. Apex of cone, AMF 59822, Magn. X3.

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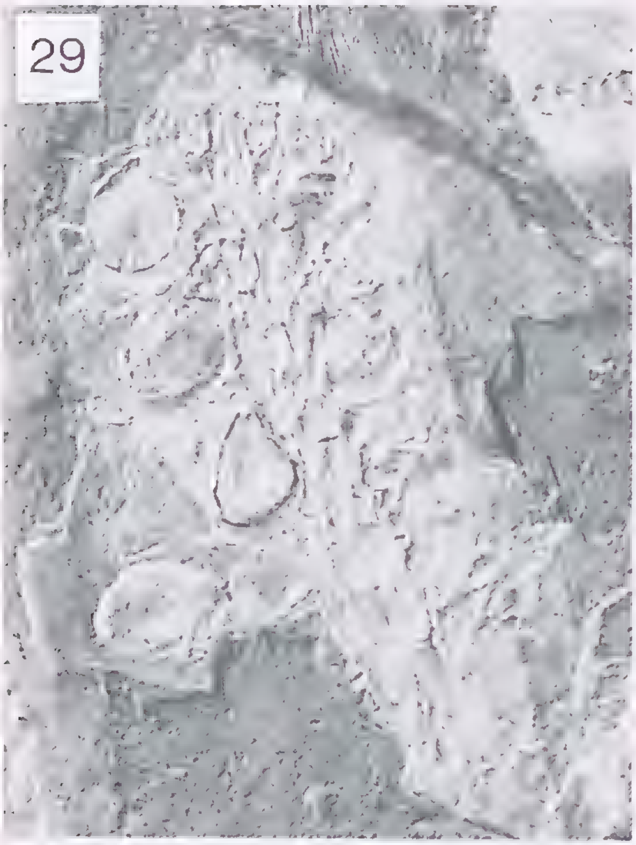

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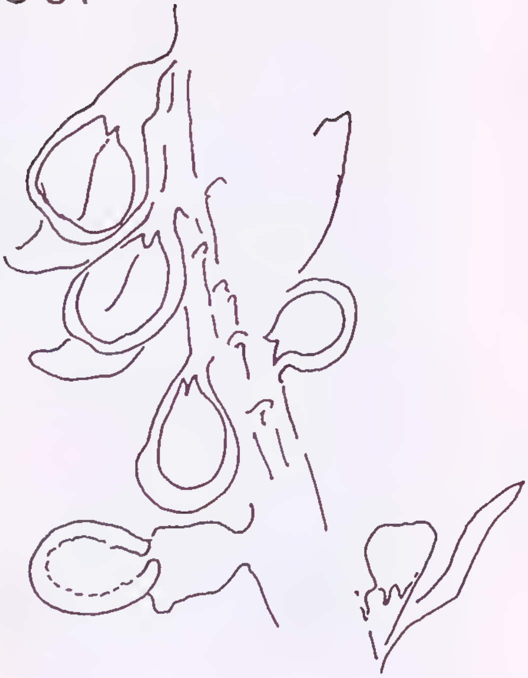

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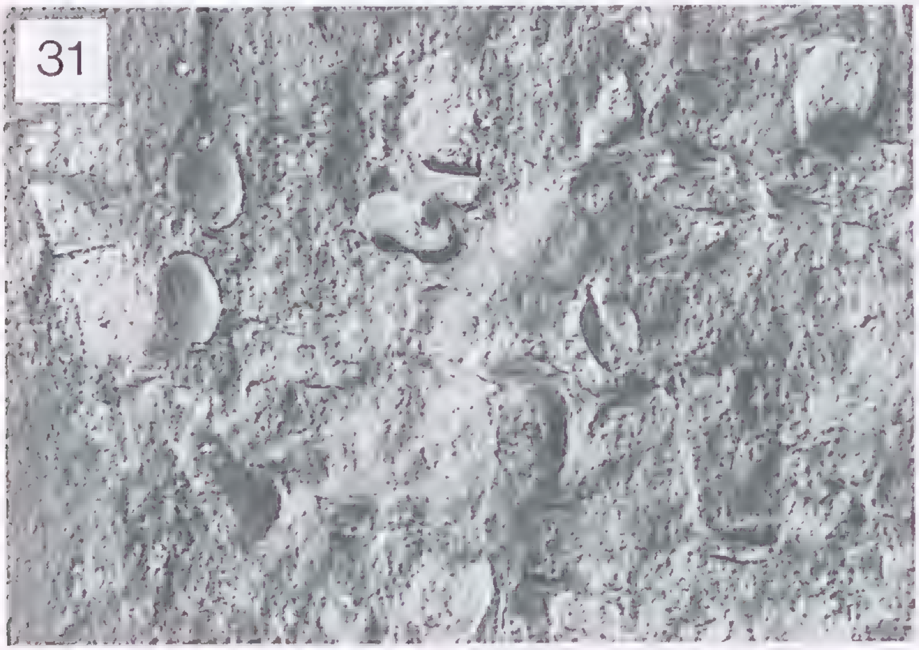


Figures 29-31. *Rissikia talbragarensis* sp. nov. Fig. 29. Base of cone. MMF 23946 Magn. X3. Fig. 30. Tracing of Fig. 39, Fig. 31. Seeds. MMF 3151. Magn. X3.

Female Cones:

"*Carnoconites australica* sp. nov." Specimens MMF 3163, 24078, 23680, 23681, 24013. Genus *Carnoconites* Srivastava 1964. Latex casts of female cones.

Male Microsporangial groups:

Specimens MMF 24150, 24148. AMF 60862, presented by Keith Holmes from his private collection.

The discovery of four cones of *Carnoconites* type in the Talbragar Fish Beds makes it possible to refer the leaves known as *Taeniopteris spatulata* to *Pentoxylon*. In India, the association of *Pentoxylon* silicified wood, *Taeniopteris* leaves and *Carnoconites* cones, is proved beyond any doubt. (Sahni 1948 summarises the evidence.) In the case of the Rajmahal fossils, petrifactions of stems, leaves and cones have given a full understanding of all the phases of the plant. The recognition of *Pentoxylon* necessitated a revision of cycadophyte classification, as the Pentoxylales are a distinct order as are the Bennetitales.

The Indian Pentoxyleae are two plants, one of "*Carnoconites compactum*" cones on "*Pentoxylon sahnii*" with leaves of "*Nipaniophyllum raoi*"; and the other of "*Carnoconites laxum*" cones on "*Nipanioxylon guptai*" stems, with leaves "broader than *Nipaniophyllum raoi*". (*Nipaniophyllum* is the generic name used for *Taeniopteris* leaves when known in petrified state.) Sahni (1948) states that "the old genus *Taeniopteris* founded by Brongniart is an artificial assemblage. As our knowledge of individual species grows, they can be transferred to their proper systematic positions."

Harris (1962) reported the occurrence of a new species of *Carnoconites* – *C. cranwelli* – in New Zealand in Lower Cretaceous strata. The New Zealand cones were associated with leaves referable to the form species *Taeniopteris spatulata* McClelland. *C. cranwelli* is very different from *C. australica* as it has much smaller cones on very long pedicels arranged in a whorl of at least twelve at the stem apex.

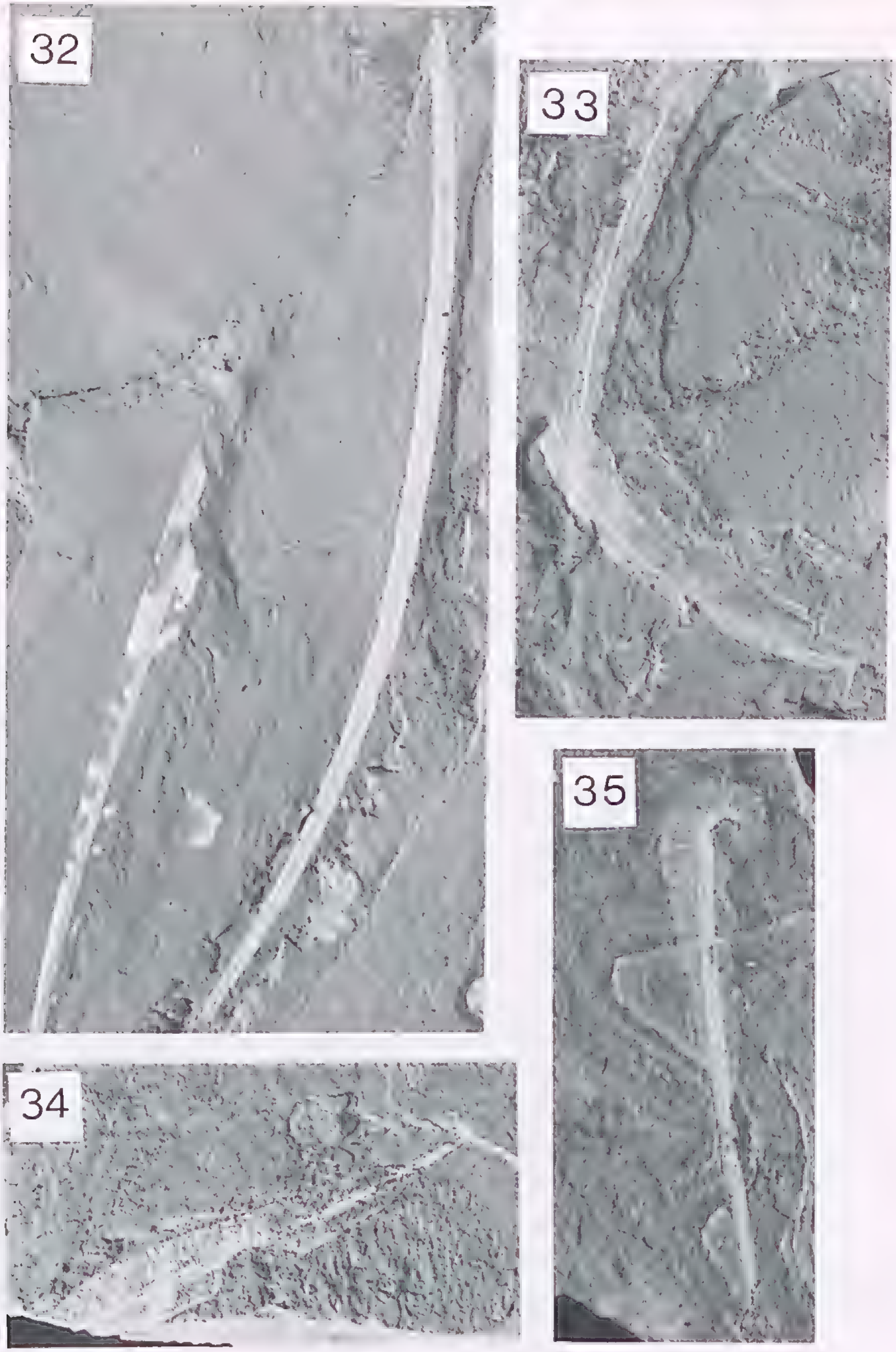
a. Leaves

The leaves of "*Taeniopteris spatulata*" in the Talbragar material vary considerably in size, from long, narrow examples more than 15 cm in length and about 0.25 cm wide, to the more commonly occurring forms which average about 1 cm in width and are proportionately less elongated. The leaf margins are parallel to most of the length of the lamina, tapering at the base into a well defined petiole in some cases, and to an acuminate or bluntly-rounded apex. A few show undulating margins. The midrib of each leaf is prominent, and lateral veins are at right angles to it and very numerous, about 25-30 per cm. Laterals fork near the midrib or further into the laminal tissue.

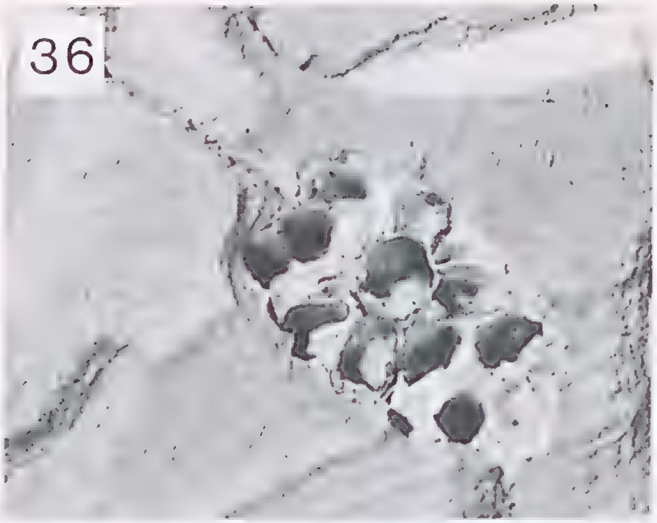
Figures 32 - 35 illustrate the range of form in leaves. In Figure 43, a leaf is seen magnified X 3 to show venation. These leaves are now assigned to *Pentoxylon australica* sp. nov.

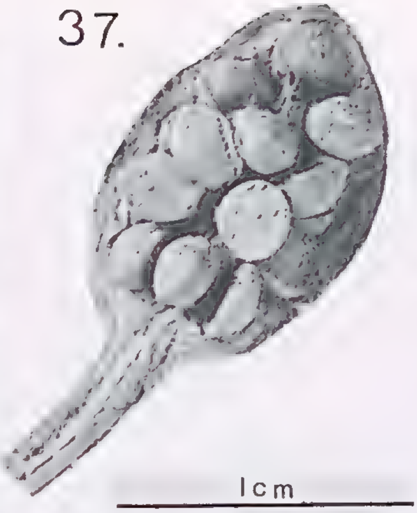
b. Female Cones

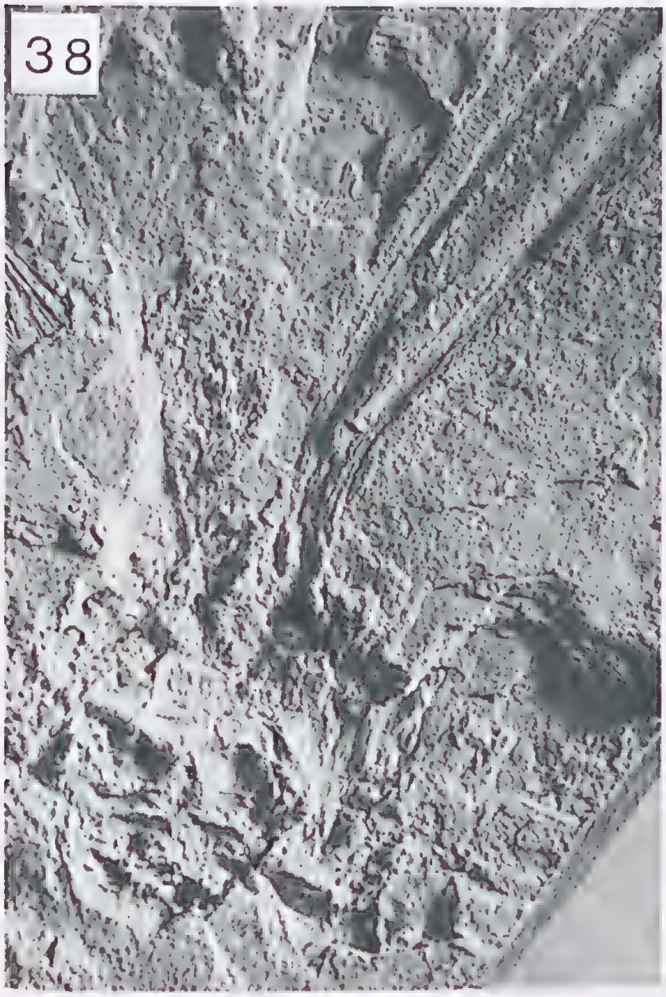
Walkom's type specimen for the "? cone", MMF 3163, figured on Pl. 6, Fig. 7 (Walkom 1921) is re-illustrated in Figure 36. The other example he figured (Figs. 4, 4a) is also referred to as MMF 3163, but it cannot be located at the Mining Museum. A latex mould made from MMF 3163 is seen in Figure 37. Moulds from two newly found examples are illustrated in Figures 39 and 40. In Figure 38 a cone and two leaves are seen attached to a stem apex.

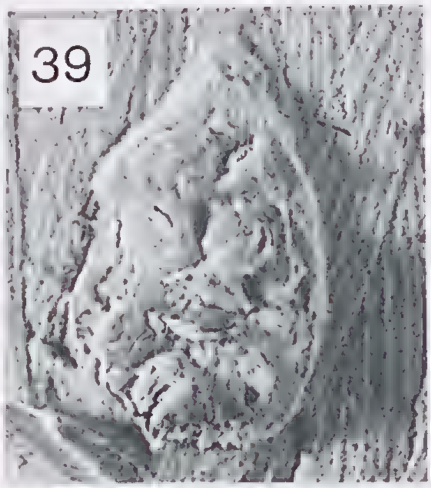


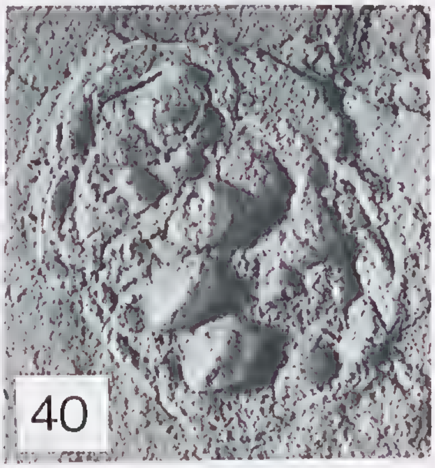
Figures 32-35. *Pentoxylon australica* sp. nov. Fig. 32. AMF 38831. Long narrow leaf. Natural size. Fig. 33. Two normal leaves. AMF 58349. Natural size. Fig. 34. AMF 58454. Leaf with petiole. Natural size. Fig. 35. AMF 59994. Leaf with curled top. Natural size.











Figures 36-40. *Pentoxylon australica* sp. nov. Fig. 36. MMF 3163. X3. Fig. 37. Latex mould from MMF 3163. X3. Fig. 38. MMF 24078. Cone and leaves attached to stem apex. X3. Fig. 39. Latex mould from MMF 23680. X3. Fig. 40. Latex mould from MMF 23681. X3.

The fructifications can be seen to be composed of sessile seeds attached to a central axis apparently in four alternating whorls of five seeds each. In Figure 37, the fleshy part of the fruit is only vaguely outlined. The stony seeds each have a median ridge. Figures 39 and 40 give a clearer impression of the "mulberry" nature of the fruit as described by Indian authors. Each seed has a fleshy sarcotesta. Cones of this sort are referred to the genus *Carnoconites* but no useful purpose can be served by doing so when they can be referred to a species which encompasses the whole plant. The name *"Carnoconites"* may be used in a descriptive role.

The Talbragar fructifications are similar in size and in the number of seeds comprising them to *C. compactum (Pentoxylon sahnii).* The male flower of *Pentoxylon sahnii* is *Sahnia nipaniensis,* and its microsporophylls are only a fifth of the size of the mature microsporophyll found at Talbragar (Figure 41), a fact supporting the erection of a new species for the Talbragar material.

Figure 38 of MMF 24078 is of particular interest and importance as it shows two leaves of *"Taeniopteris spatulata"* and a *Carnoconites australica* cone attached to a stem apex. A second specimen, MMF 24013, also shows two narrow leaves and a cone attached to a stem apex, removing any doubt about the association. The pedicel attaching the cone to the stem apex is short.

c. Microsporangia

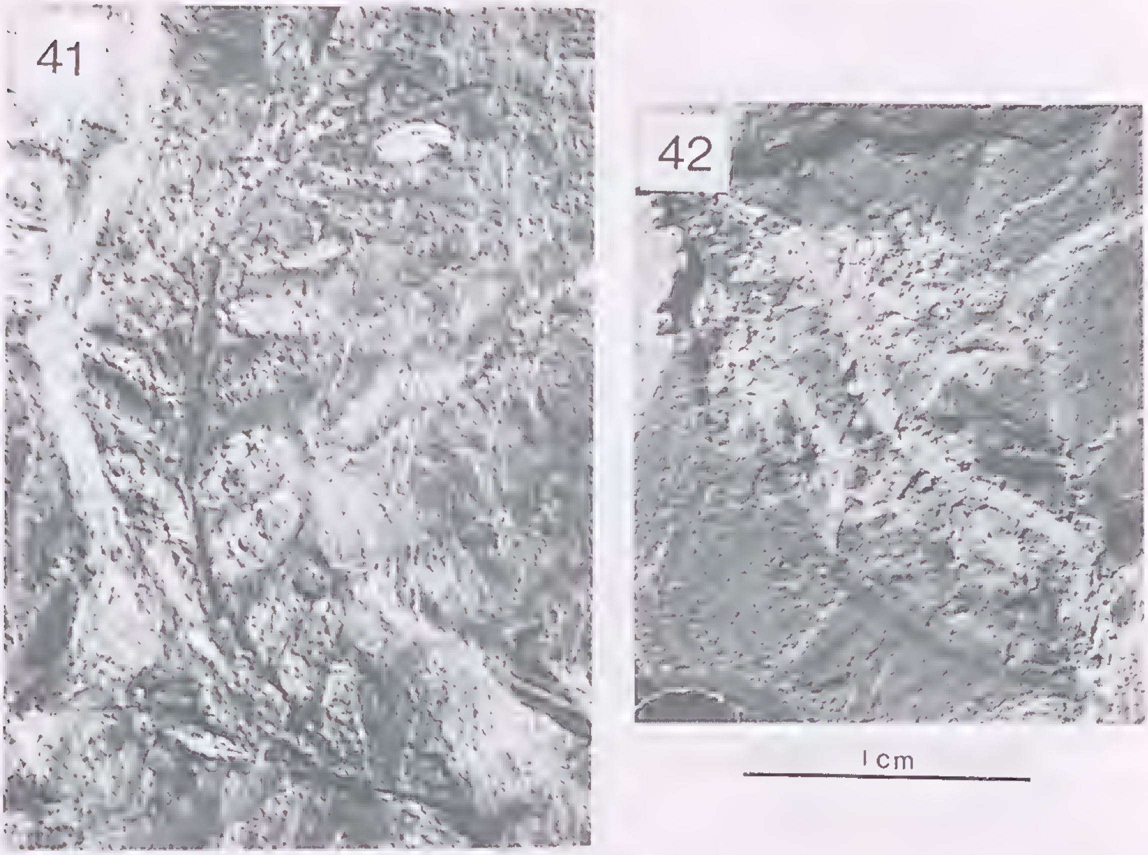
In the examination of the Cullen Collection, two examples were found of aggregations of microsporangia. One of these is illustrated in Figure 42. It probably represents an immature example of the male phase of *Pentoxylon australica.* The Australian Museum is most grateful to Mr Keith Homes of Wellington for presenting a specimen AMF 60862 to complete the information on *Pentoxylon australica.* It had been in his collection for some time, but as *Pentoxylon* had not been recognised in Australia, its significance has not been appreciated. This specimen, Figure 42, contains a filiform microsporophyll with 14 pear-shaped, unilocular sporangia borne on short pedicels. Apart from the size of the specimen, which is five times larger than the microsporophylls recorded for *Sahnia nipaniensis,* it is similar in form to the individual microsporophylls of the male flowers of *Pentoxylon* in India (Vishnu-Mittre 1953).

### 4. Conifer foliage — "**Brachyphyllum** sp. Walkom 1921"
Figures 43-46

*Allocladus cribbii* Townrow 1967a.
Classification: Townrow 1967a.
Coniferales incertae sedis.
New classification: Coniferales. Podocarpaceae.

Branching conifer twigs with closely adpressed, triangular leaves. Specimen AMF 16443, illustrated in Figure 43, shows a typical slender, forking branchlet. Townrow described the vegetative organs and had no evidence on cones to allow allocation to a family.

Specimen AMF 59988 (counterpart 59989), Figures 44 and 45, show a small twig of the conifer which bears three cones at its apex. Preservation is poor and little detail of the cones can be seen. A specimen was found (AMF 59991) in which three small cones are preserved in a symmetrical tripartite arrangement (Fig. 46). The cones are detached, but they are believed to be referable to *Allocladus cribbii.* They are the same size and shape, and correspond in all discernible details.



Figures 41 & 42. Microsporophylls of *Pentoxylon australica* sp. nov. Fig. 41. AMF 60862. Magn. X3. Mature microsporophyll. Fig. 42. MMF 24150. Magn. X3. Young microsporophylls.

Details of cones are not clear, but knowledge of their arrangement is sufficient to identify the affinities of the conifer. Trimerous symmetry is characteristic of Podocarpaceae. An examination of living podocarps emphasises this — the New Caledonian *Dacrydium balanse* is a similar conifer, with closely adpressed foliage and bearing three cones at the end of slender branchlets. *Dacrydium araucarioides, Acmopyle pancheri* and *Decussocarpus comptonii* of the Podocarpaceae show similar cone arrangements. (See de Laubenfels 1972 for illustrations of all these species.) *Dacrydium novogunense* of New Guinea has similar foliage.

Podocarpaceae is the most important family of conifers in the Southern Hemisphere. Although there are some representatives north of the Equator they are assumed to have arrived relatively recently, and the family is believed to have originated in the South.

### 5. Conifer foliage — "?**Pagiophyllum peregrinum** (L. & H.) Walkom 1921"

Figures 48, 49, 51

*Allocladus milneanus* (Ten. Woods) Townrow 1967a

Figures 48, 49, 51 show conifer foliage which is referred to this species. Foliage is variable, leaves from narrow (Fig. 48) to foliose (Fig. 49), and until cones are found attached and the foliage can be placed in a family, it should be regarded as a form-species and not necessarily related to *Allocladus cribbii* which is now known to be Podocarpaceous.

### 6. Conifer foliage — **Elatocladus australis** (Frenguelli)

Figure 47

Figure 47 of AMF 58303 shows a rare type of foliage which does not belong to any of the conifer species so far described. It is closest in appearance to *Elatocladus australis*, a species which Townrow considered valid and to which he referred some conifer foliage from New South Wales (Townrow 1967b).

### 7. Cycad frond — **Nilssonia compta** (Phill.) Bgt.

Figure 52

Figure 52, AMF 59980, shows a small cycad frond in The Australian Museum collection from Talbragar. A similar frond was found in the Cullen Collection.

### 8. **Selaginella** sp.

Figure 53

Figure 53 shows a portion of specimen AMF 25679 in which a delicate branching plant occurs. The stems are clothed in small leaves, and small side branches with larger leaves, appear to bear round ? fruits. This specimen is doubtfully assigned to *Selaginella*.

### 9. **Onychiopsis** sp.

Figure 50

A very small, repeatedly dichotomising, fragment of a fern is seen in Figure 50, specimen MMF 24147. It is referred to the genus *Onychiopsis* Yokoyoma 1890, and it resembles the ultimate segments of *Onychiopsis tenuiloba* Lorch (1967). The fragment is only 1 cm long, with smallest segments 2 mm in length, so no close identification can be made. No fern of this sort has been described from the Jurassic in Australia before.

## ACKNOWLEDGEMENTS

Mr John Fields of the Photography Department of The Australian Museum photographed the specimens. I acknowledge with gratitude his most valuable contribution to this paper.

I am grateful to Dr John Pickett, Principal Research Officer of the Mining Museum, for making arrangements enabling me to examine the Cullen Collection, and for the loan of specimens from it and from the other collections of the Mining Museum.

Mr D. Macgillivray and staff of the National Herbarium were most helpful in my study. of living plants relating to the Talbragar fossils and kindly lent literature.

I wish to thank Dr Alex Ritchie, Curator of Fossils, of The Australian Museum for his advice and assistance.

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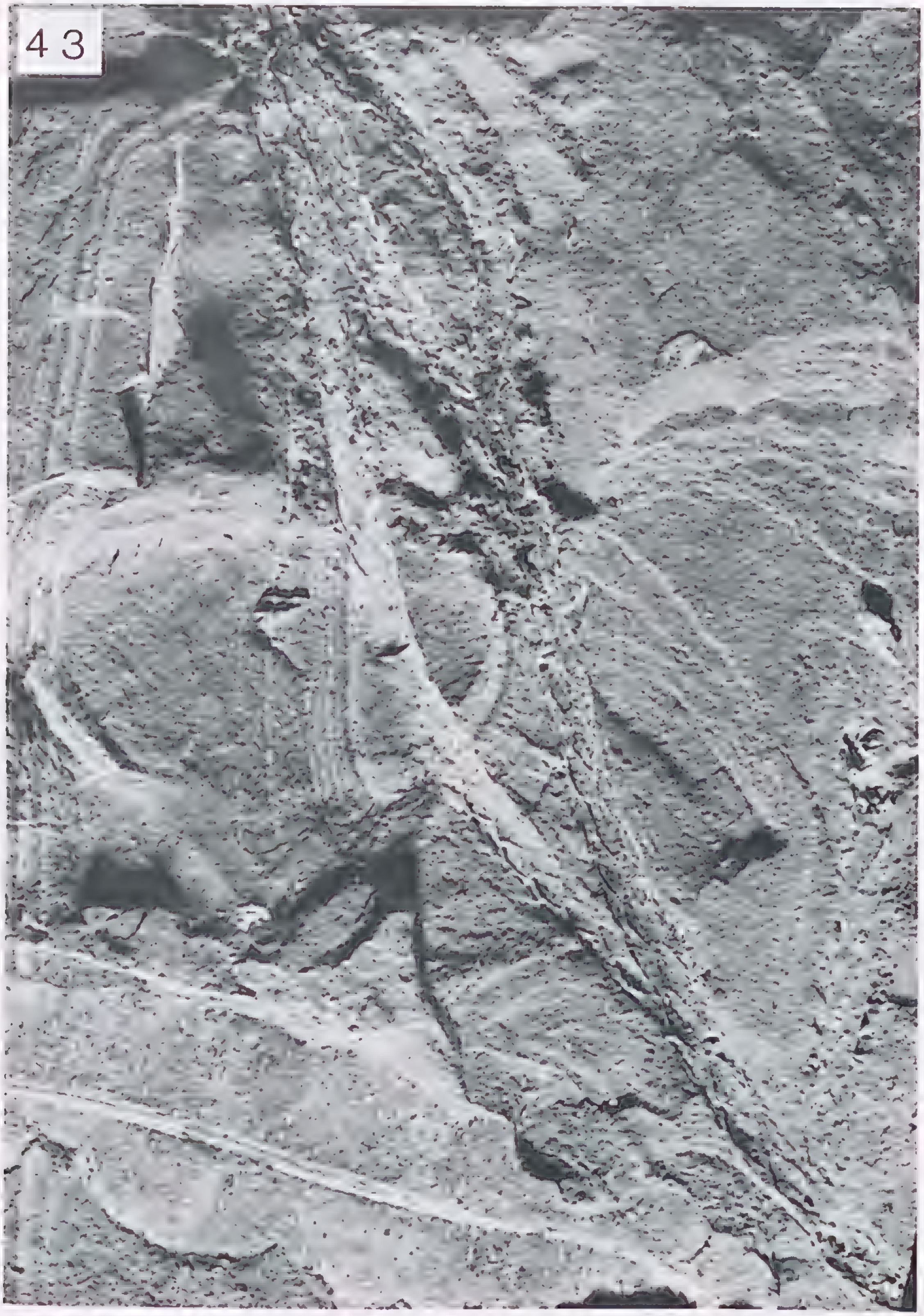
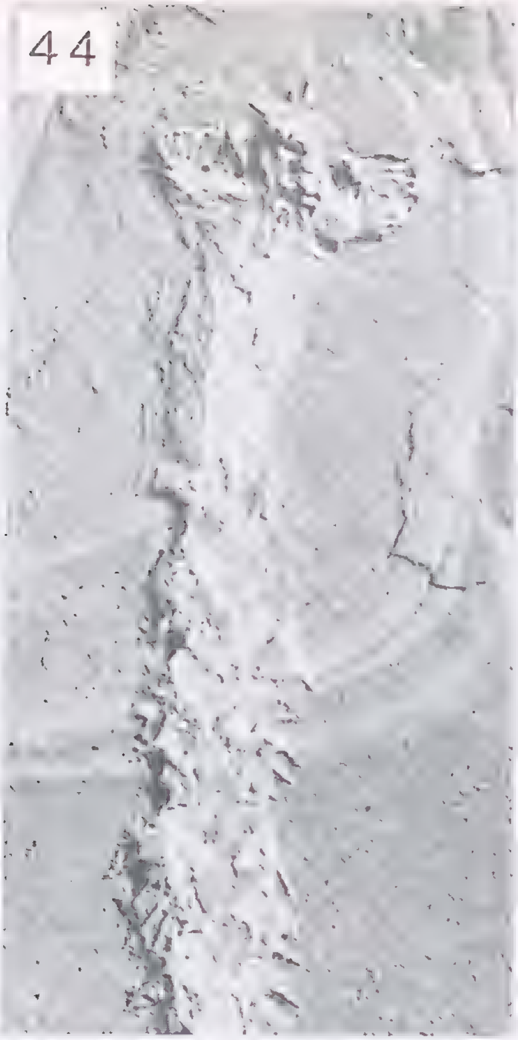


Figure 43. Conifer twig — *Allocladus cribbii* Townrow, and leaf of *Pentoxylon australica* sp. nov. showing venation. AMF 16443. Magnification X3.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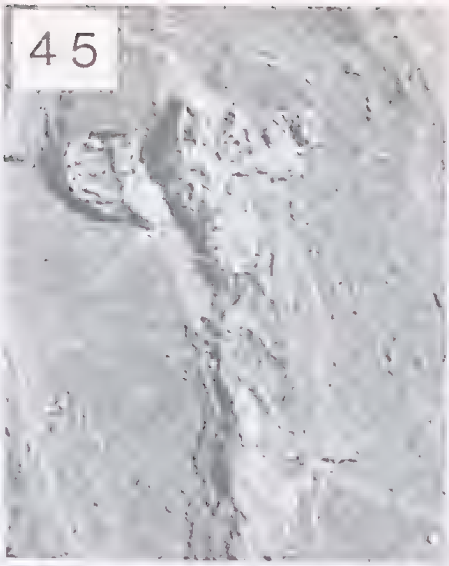
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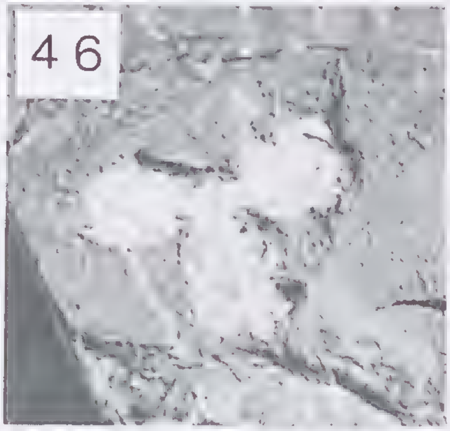
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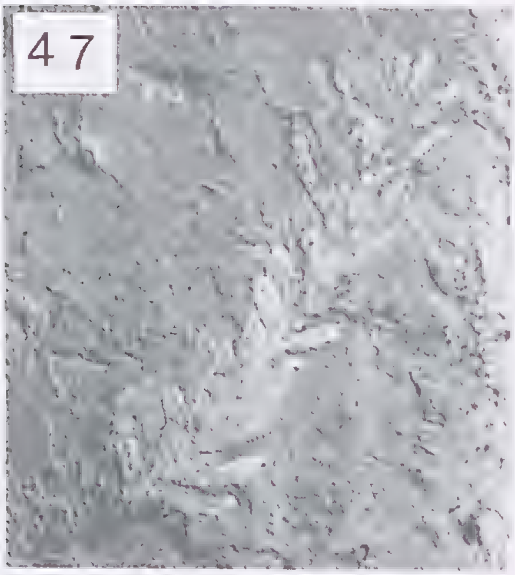
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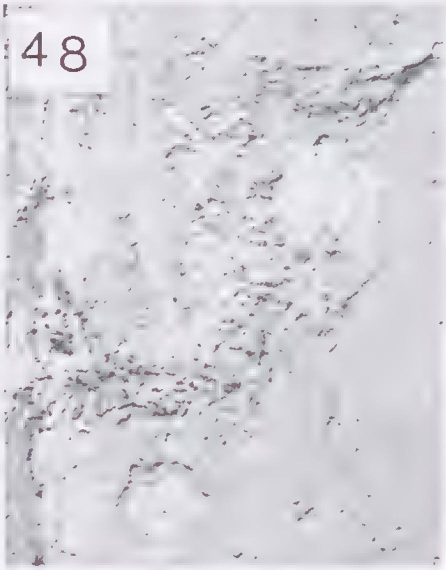
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Figures 44 - 46. *Allocladus cribbii* Townrow. Magn. X3. Fig. 44. AMF 59988. Twig terminating in three cones. Fig. 45. AMF 59989. Counterpart. Fig. 46. AMF 59991. Three cones. Figure 47. *Elatocladus australis* Frenguelli. AMF 58303. Natural size. Figure 48. *Allocladus milneanus* (Ten.Woods) Townrow. Natural size. MMF 23941.

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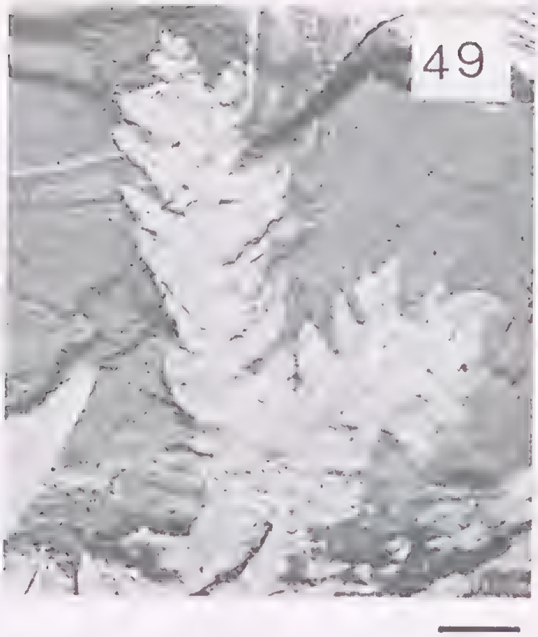

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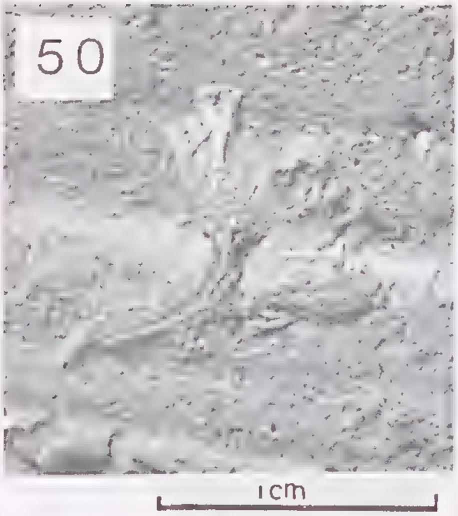

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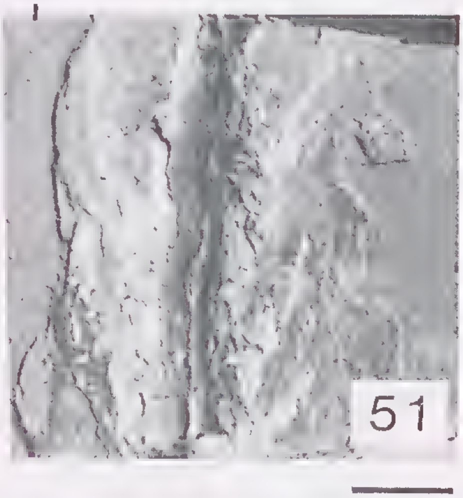

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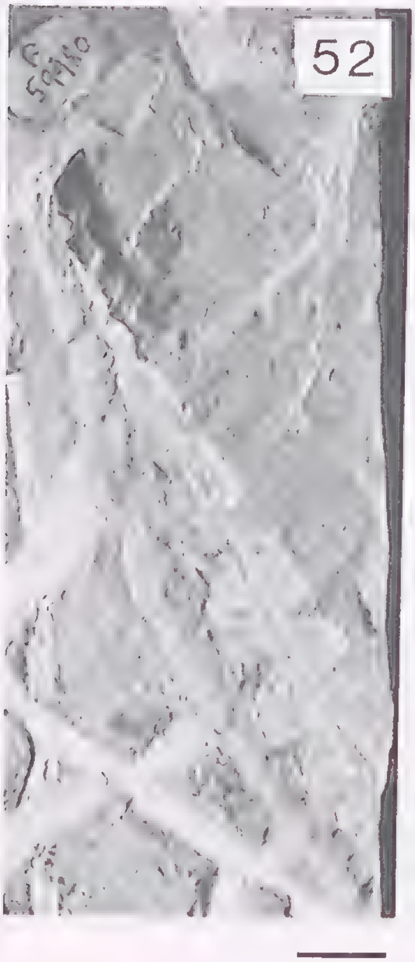

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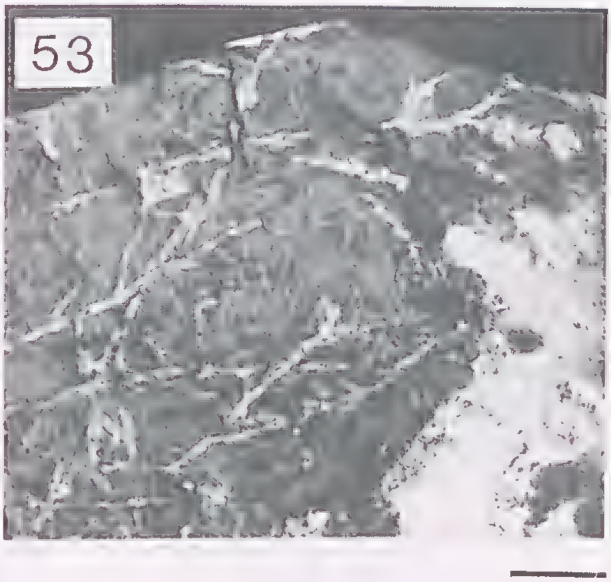

Figures 49 & 51. AMF 59981, 59993. *Allocladus milneanus* (Ten.Woods) Townrow. X1. Figure 50. *Onychiopsis* sp. MMF 24147. X3. Figure 52. *Nilssonia compta* (Phill.) Bgt. AMF 59980. Natural size. Figure 53. *Selaginella* sp. AMF 25679. Natural size.

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Manuscript accepted for publication 21 February, 1980

# *CYLOMEIA UNDULATA* (BURGES) GEN.ET COMB.NOV., A LYCOPOD OF THE EARLY TRIASSIC STRATA OF NEW SOUTH WALES

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## SUMMARY

*"Taeniopteris undulata* Burges" leaves are identified as lycopod leaves which were borne in flat, plate-like crowns on *Pleuromeia*-like plants which are given the new generic name *Cylomeia*. "*Pleuromeia longicaulis* (Burges) Retallack" is referred to the same genus. It is suggested that *Cylomeia undulata* (Burges) might have borne cones recently described as *Skilliostrobus* Ash 1979, in the same manner as *Cylomeia longicaulis* (Retallack) bore *Cylostrobus* cones.

## AN EARLY TRIASSIC LYCOPOD

Burges (1935) described as *Taeniopteris undulata* long, narrow leaves with a pronounced midrib (two median grooves) and undulating margins in his account of the Narrabeen Flora of New South Wales. Leaf fragments of this type are fairly common in the Narrabeen Group sediments which outcrop in many localities in Sydney's Northern Beach suburbs from Narrabeen to Palm Beach. Similar long, narrow leaves with less obvious midribs and without undulating margins, occur in great profusion locally in some areas, and have been assigned to *Pleuromeia longicaulis* by Retallack (1975) in his reconstruction of that plant.

In 1977, a specimen was obtained by The Australian Museum, prompting this investigation which has resulted in its identification as a whorled lycopod leaf crown comprising leaves of "*Taeniopteris undulata*" type. The specimen AMF 58791 was obtained from Early Triassic roof shales above the Upper Permian Bulli Seam in the Bellambi Colliery (K panel), Wollongong. It is beautifully preserved as an impression with a film of carbon on the surface, and shows a whorl of ribbon-like leaves which are attached to the stem apex in several layers, forming a plate-like crown 18 cm in diameter, slightly concave in the centre. Unfortunately no cell structure is preserved. The leaves are broken off, or interrupted by the edges of the specimen at a length of 8 or 9 cm. They average 5 mm in width (Figure 1).

The leaves have parallel margins and are without visible midribs for most of their preserved length, but towards their extremities the margins start to undulate and the midribs become more pronounced (Figure 2). If the leaves had been preserved as broken up fragments, as is usually the case in plant fossils, the undulating distal parts would have been consistent with *Taeniopteris undulata* and the proximal parts indistinguishable from *Pleuromeia longicaulis*.

A new genus *Cylomeia* is erected as this specimen cannot be accommodated in any existing genus of lycopods for reasons detailed below. The name is derived from *Lyco* — reversed as in *Cylostrobus* — and *meia* a diminutive as in *Pleuromeia* to indicate the dwarf-tree nature of the lycopod, and also to indicate its relationship with those plants.

A second specimen showing a less complete crown of more mature leaves was found in the Wollongong University collection by Dr. A. Wright, and presented to The Australian Museum. It came from the same horizon and general locality in the Bellambi Colliery, Wollongong. This specimen, AMF 60882, shows approximately ten broader

Records of The Australian Museum, 1981, **Vol. 33 No. 16,** 723-734, Figures 1-10.

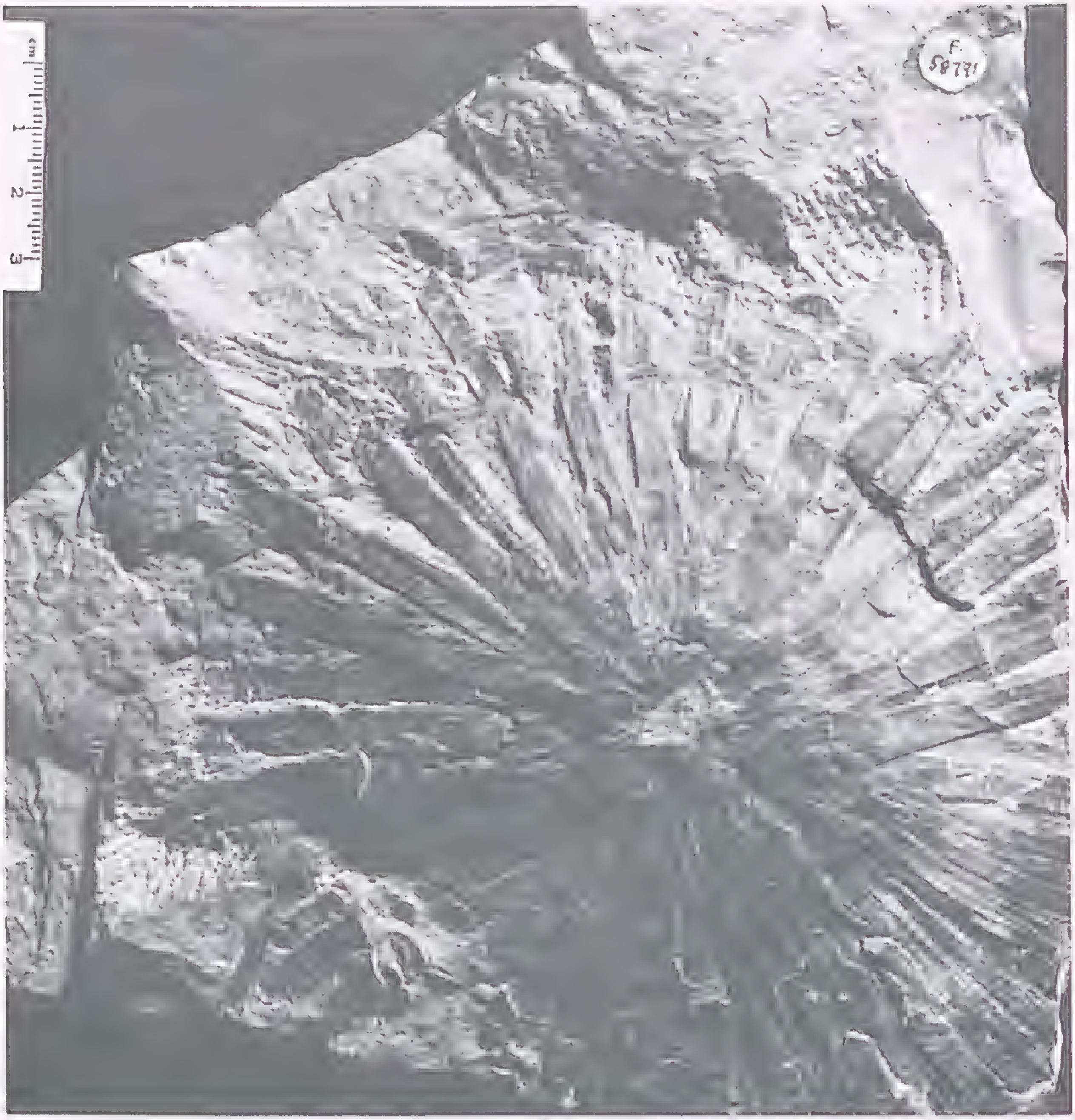
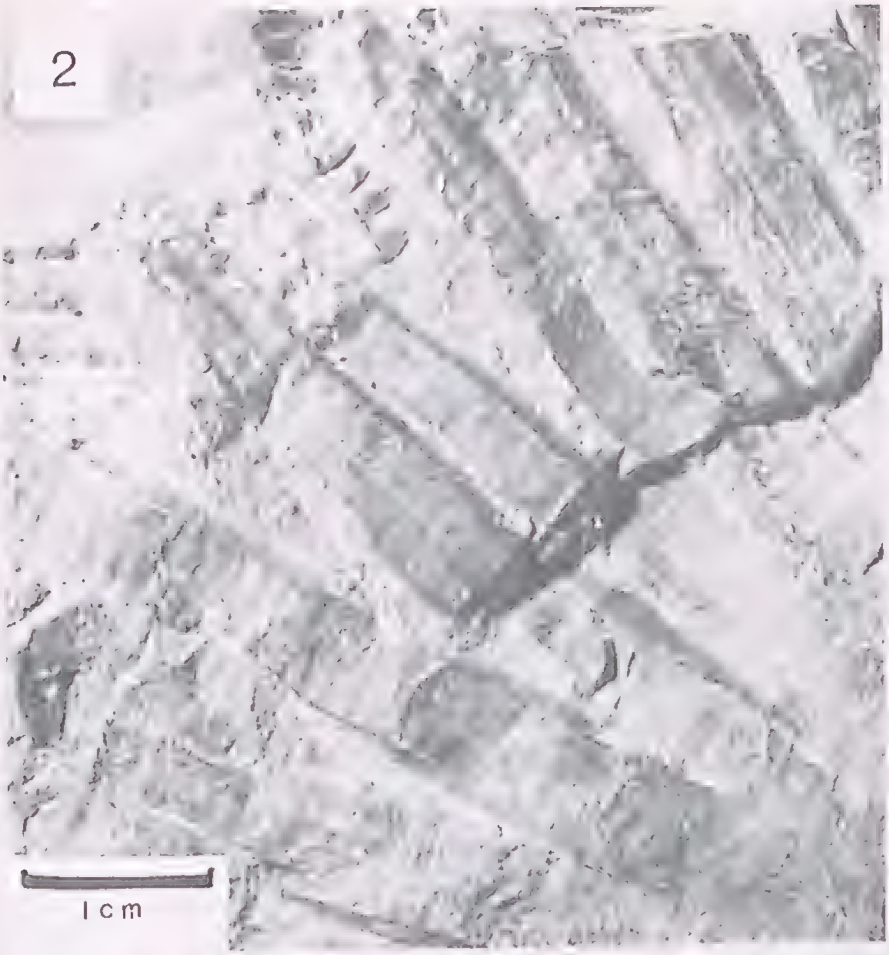
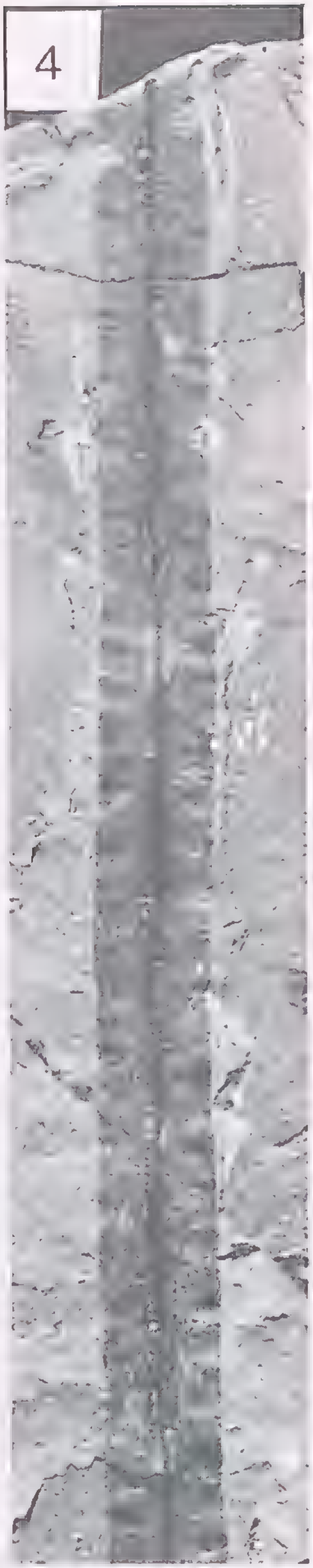


Figure 1. Specimen AMF 58791. Natural size. Plate-like crown of ribbon leaves.





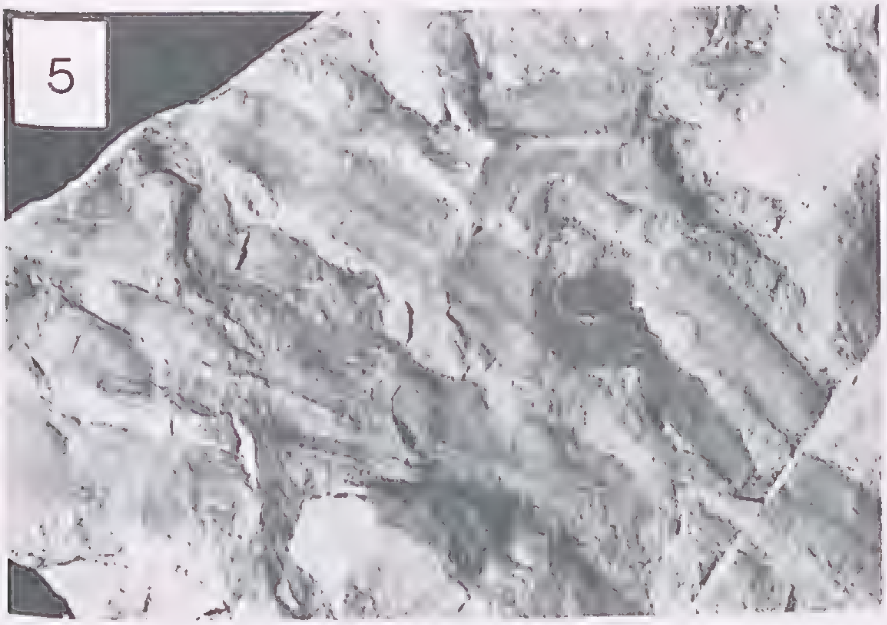


Figure 2. AMF 58791. magn. X 2. Part of leaf whorl.
Figure 4. AMF 59987. Natural size. Part of long leaf. Avalon, N.S.W.
Figure 5. AMF 39862. Natural size. Leaves. Rylstone. N.S.W.

leaves, each slightly more than 1 cm wide, attached to the rim of a concavity which represents the stem apex. The leaves have strongly undulating margins and are manifestly *"Taeniopteris undulata"* throughout their entire length. A tracing of this specimen is seen in Figure 3.

Re-examination of the Triassic collections of The Australian Museum has revealed two more examples of leaf whorls, both poorly preserved, one a coal sample with no locality information, presumed to be from a South Coast Colliery and of Upper Permian age (the coal seam being just below the roof shales which contained the other specimens), and the other from Triassic shale (? Ashfield Shale) from an old brick pit at Erskineville, Sydney (AMF 16178). The range of *Cylomeia undulata* leaf whorls is thus shown to be from Upper Permian to probably Middle Triassic.

Unattached, long, narrow leaves of *"Taeniopteris undulata"* from Avalon (Figure 4) and from Early Triassic strata at Rylestone New South Wales (Figure 5) show the diversity of size and the wide geographical range of the specimens. They are referred to *Cylomeia undulata*. A leaf of *"Taeniopteris undulata"* occurs in the Upper Permian assemblage at Merewether Beach, Newcastle (AMF 26060) so the unattached leaves are also seen to range from Upper Permian into Triassic. Leaves of this type are known to reach 50 cm in length, with undulating margins throughout, and it seems that only the part of each closest to its attachment to the stem is smooth, and then probably only in immature leaves.

The very numerous leaves of *"Pleuromeia longicaulis* (Burges) Retallack" occurring in some layers of Narrabeen Group shales are now assigned to *Cylomeia longicaulis* (Retallack). Associated with these leaves, and with the rarer leaves of *Cylomeia undulata,* are lycopod stems which are woody and approximately 1 - 1.5 cm in diameter (before compression). Some of these show widely spaced, single leaf-traces in ascending spiral arrangement. These are also rhizophores, some in continuity with stems similar to those with leaves attached in Retallack's *"Pleuromeia longicaulis"*. The rhizophores are elongated and unlobed, or more buttress-like and somewhat lobed, the latter occurring in numbers in some localities in growth position, preserved as casts which separate from their impressions (Figure 7). The rhizophores are referred to *Cylomeia,* but not to any species as rhizophores of similar lycopods would be expected to be of a general type, as *Stigmaria* are the general root type for species of *Lepidodendron*.

Very large numbers of lycopod cones which were described by Helby and Martin (1965) as *Cylostrobus,* are associated with the leaves, stems and rhizophores in Narrabeen Group sediments. Retallack (1975) reconstructed *Pleuromeia longicaulis* (Burges) from the evidence of non-undulate leaves, stems, rhizophores and cones of *Cylostrobus,* and believes that all the *Cylostrobus* species separated by Helby and Martin are best considered as one species — *Cylostrobus sydneyensis* (Walkom) — as only the size varies. Figure 8 illustrates part of a specimen with numbers of *Cylostrobus* cones associated with numerous *Cylomeia longicaulis* leaves from Avalon. Retallack's reconstruction of *Pleuromeia longicaulis* is illustrated in Figure 6 in a comparison with *Cylomeia undulata.*

Retallack's use of the genus *Pleuromeia* for his species cannot be justified. *Pleuromeia* is completely known from a study of the northern hemisphere fossils assigned to it and differs in significant details. If Retallack's interpretation and reconstruction are correct, and the ubiquitous association of the *Cylostrobus* cones and the vegetative organs leaves little doubt, then a new genus is indicated. The most

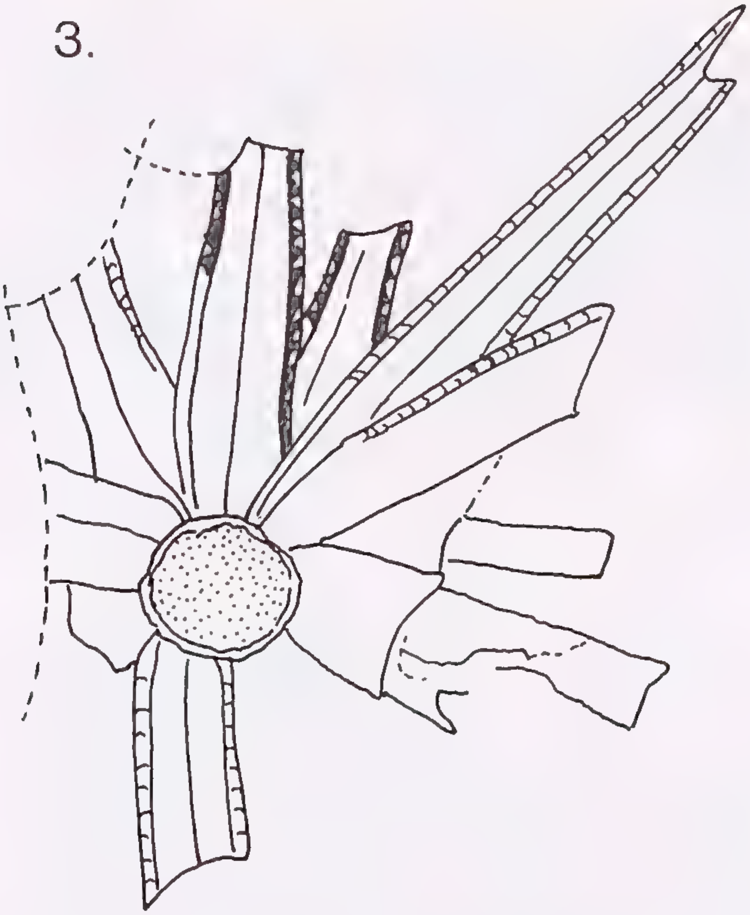


Figure 3. Tracing of incomplete whorl of *Cylomeia undulata*. Natural size. Specimen AMF 60882.

fundamental difference warranting generic separation is in the cones. *Pleuromeia* is dioecious (it has separate plants bearing male and female cones). The sporophylls bear unilocular sporangia, the megasporangia contain trilete megaspores, and the microsporangia bear monolete spores (as in *Cylomeia*). There has been some speculation about whether the sporangia were borne on the upper or lower surface of the sporophylls in *Pleuromeia* but Chaloner (in Boureau 1967) accepts that Neyburg (1961) has proved that they are on the upper surface of sporophylls as in *Cylomeia*. The mega- and microsporophylls of *Pleuromeia* are more or less round in shape and the "cone" is described as the "fertile region of the stem". There is no way that the cones of *Cylostrobus* could be described as "fertile regions" of stems. They are highly organised cones distinct from the rather lax aggregations of sporophylls in *Pleuromeia*. The plants of *Cylomeia* are monoecious, each cone has its distal sporophylls bearing unilocular microsporangia, while the lower (proximal) sporophylls have megasporangia. The sporophylls are true cone scales with keels and upturned apices. (Neyburg's 1961 *Pleuromeia rossica* is considered by the author to be excluded from *Pleuromeia* and distinct from *Cylomeia* and cannot be considered further here without access to the specimens from Russia.)

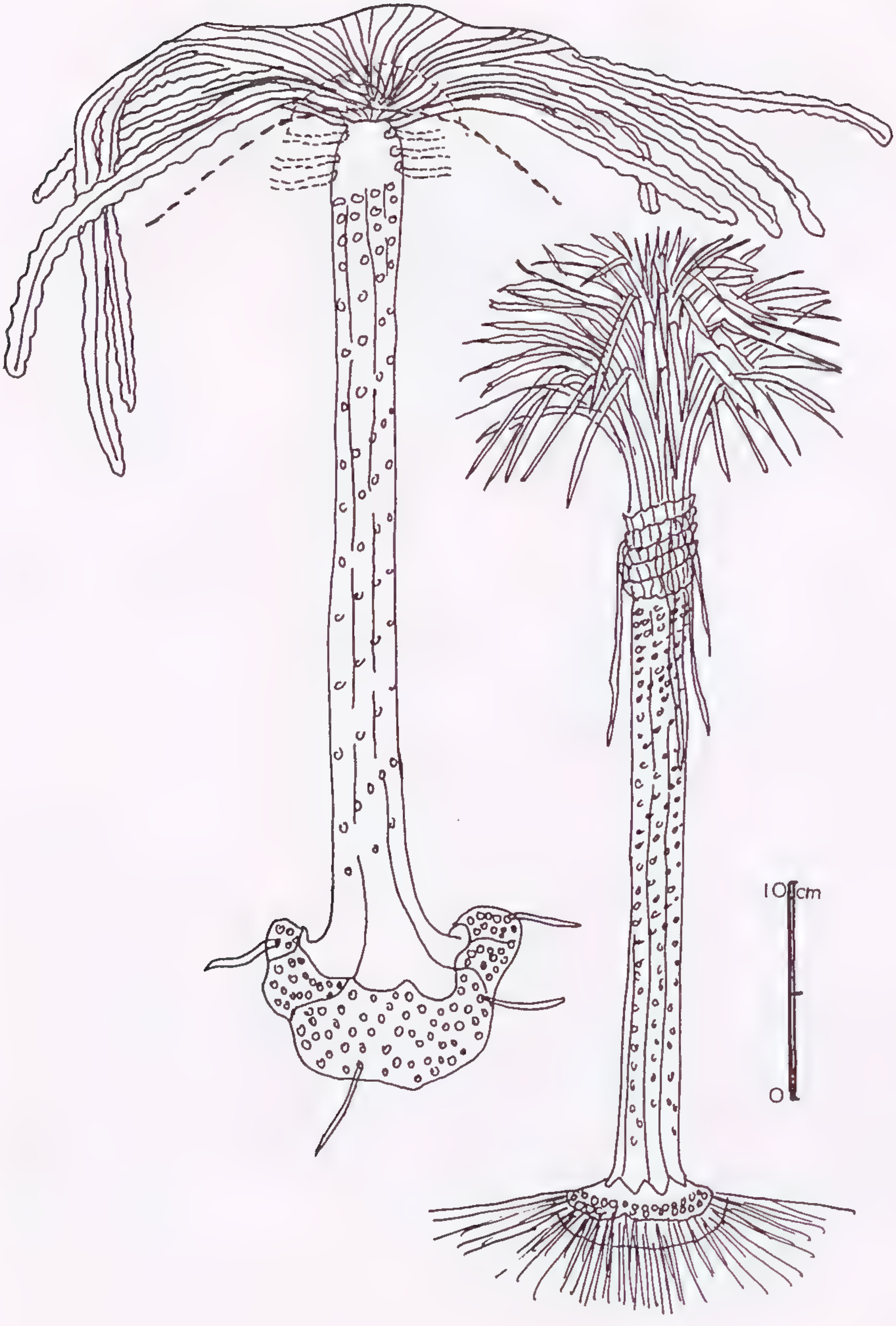
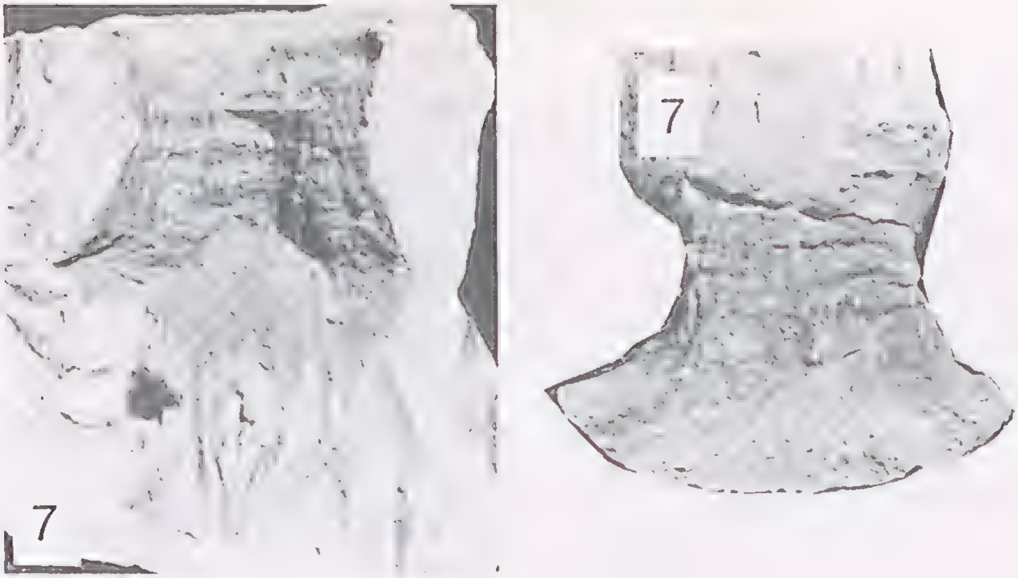


Figure 6. Reconstructions of *Cylomeia undulata* and *Cylomeia longicaulis* (after Retallack, 1975).



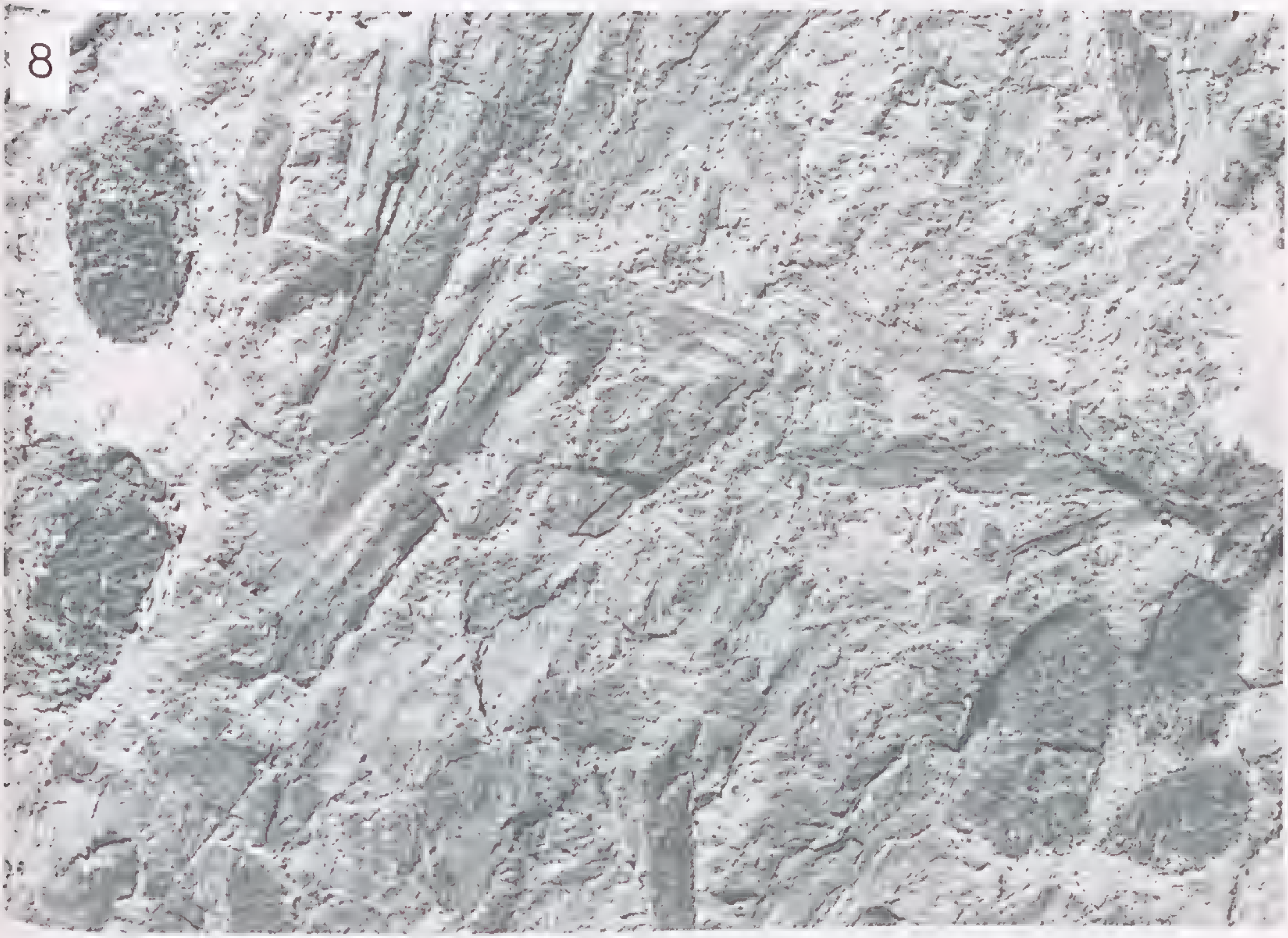


Figure 7. Rhizophore of lycopod. Natural size. AMF 59985 impression. AMF 59986 cast separated from impression.
Figure 8. *Cylomeia longicaulis* leaves and *Cylostrobus sydneyensis* cones. AMF 59975, magn. X 1.5.

Supporting the separation of *Cylomeia* from *Pleuromeia* on evidence from cones, are less significant differences in vegetative structure. *Pleuromeia* has two scars on the leaf base, either double leaf trace or parichnos scars, and there is only one leaf trace on each leaf base in *Cylomeia* (see Fig. E. p.18, Retallack, 1975). The rhizophores of *Pleuromeia* are strongly four-lobed by dichotomy, those of *Cylomeia* are not.

It is becoming increasingly evident, as detailed knowledge of Australian plant fossils accumulates, that Australian Late Palaeozoic and Mesozoic plants have Southern affinities and cannot be equated with their Northern Hemisphere relatives and contemporaries.

As the form of the plant in *Cylomeia undulata* is different from *Cylomeia longicaulis* with its brush-like tuft of leaves, it is probable that its cones, which would have arisen at the centre of the leaf whorl in the concavity at the top of the stem, would have been different too. The only other lycopod cones or cone scales in the Narrabeen Group are the recently described *Skilliostrobus* Ash 1979. In essential structure these cones are the same as *Cylostrobus*, having the distal half composed of microsporophylls, and the proximal half of megasporophylls. Sporangia are unilocular, spore types the same as in *Cylostrobus*. The sporophylls are different in appearance because they have an elongated limb which is bifid at the apex. The cones have a "sunflower-like" appearance when compressed. It could be argued that *Skilliostrobus* should have been described as a species of *Cylostrobus*. It seems possible that *Cylomeia* bore *Skilliostrobus* cones. This theory is given support by evidence from the Early Triassic Blina Shale in the Canning Basin, Western Australia (White 1976) in which stems and rhizophores indistinguishable from those of the Narrabeen Group are associated with scales which are now referable to *Skilliostrobus*.

### Definition of **Cylomeia** gen. nov.

Classification: (Chaloner in Boureau 1967)

Class: Lycophyta.

Order: Lepidodendrales.

Family: Lepidodendrales incertae sedis.

Genus: *Cylomeia*

Dwarf; woody stemmed lycopods, probably attaining about a metre in height, with single, erect stem arising from a rhizophore (somewhat lobed or unlobed) bearing stigmarian rootlets. Plants growing in swamps in monodominant thickets, occupying the mangrove niche of present day tidal or lagoonal habitats (Retallack, 1975) in Early Triassic horizons. Plants having the appearance of small palms, with naked trunks ornamented with ascending spiral leaf trace scars. Each leaf trace a single scar in the centre of the leaf base scar. Leaves attached to the stem near the top, either in a brush-like arrangement or in a flat, plate-like crown. Leaves ribbon-like, attaining considerable length in proportion to the height of the plants, each having two stomatal grooves.

Plants monoecious, bearing highly organised cones in which the proximal sporophylls bear unilocular megasporangia, and the distal sporophylls bear unilocular microsporangia. Sporangia on upper surface of sporophylls. Sporophylls are keeled with upturned apices — each being a well developed cone scale. Cone scales closely inserted on the cone axis, many in each whorl. Megaspores are trilete, microspores monolete.

Three species are so far recognised:

a. *Cylomeia undulata.* Plant with plate-like crown of *"Taeniopteris undulata* (Burges)" leaves. Cones possibly *Skilliostrobus* Ash.

b. *Cylomeia longicaulis* (Retallack). Plant with brush-like tuft of smooth, strap-like leaves. Cones *Cylostrobus sydneyensis* Helby and Martin.

c. *Cylomeia sp.* From the Canning Basin, Western Australia, in Blina Shale (White 1976)
Specimens BMR F 23662, 23660, 23704 — Stems
BMR F 23786 — Rhizophore
BMR F 23644, 23715 — Cone Scales cf. *Skilliostrobus.*

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## ADDENDUM

Since this manuscript went to press, specimens have been found of another species of *Cylomeia* which is named *Cylomeia capillamentum* sp. nov. because it has a wig-like circlet of linear leaves surrounding its terminal cone. The specimens are part of a collection from Narrabeen Group shales at Long Reef, Narrabeen, made by Dr John Talent of Macquarie University and presented to the Australian Museum in July, 1980. There are five examples of *Cylomeia capillamentum*. Three are illustrated in Figures 9 (F 60890) and 10 (F 60891). Each has a large circular cone impression in the centre measuring 6, 7.5 and 6 cm in diameter, and the very numerous hair-like leaves of the circlet are up to 10 cm in length and less than 1 mm wide. There is some carbonaceous material on some of the cones and leaves and cuticle and spore preparations will be attempted. Preliminary examination of the carbon film on one cone kindly undertaken by Dr R. J. Helby showed only immature microsporangia. Dr Helby (pers. commun.) had believed that some of the relatively rare, large, spherical cones he had examined when studying *Cylostrobus* for his publication (1965) were distinct from the range now included by Retallack in *Cylostrobus sydneyensis*, and is now confident that these are the same as those borne by *Cylomeia capillamentum*.

### Definition of **Cylomeia capillamentum** sp. nov.

A small, arborescent lycopod, presumed to be similar in habit to *Cylomeia undulata* and *C. longicaulis,* with densely inserted hair-like leaves up to 10 cm long, forming a multi-layered whorl at the top of the axis. Large spherical cone of *Cylostrobus* type with a diameter of up to 7.5 cm borne in the hollow at the top of the axis, with small, very numerous sporophylls, at least 20 tiers high, in close, ascending-spiral arrangement. Up to 100 sporophylls in a equatorial whorl. Cones apparently spherical, in contrast to the oval cones of *Cylostrobus sydneyensis* which are borne by *Cylomeia longicaulis*, and larger than the top of the range included in that species when mature. The cones of the species are named *Cylostrobus capillamentum* sp. nov.

Manuscript accepted for publication 21 February, 1980.

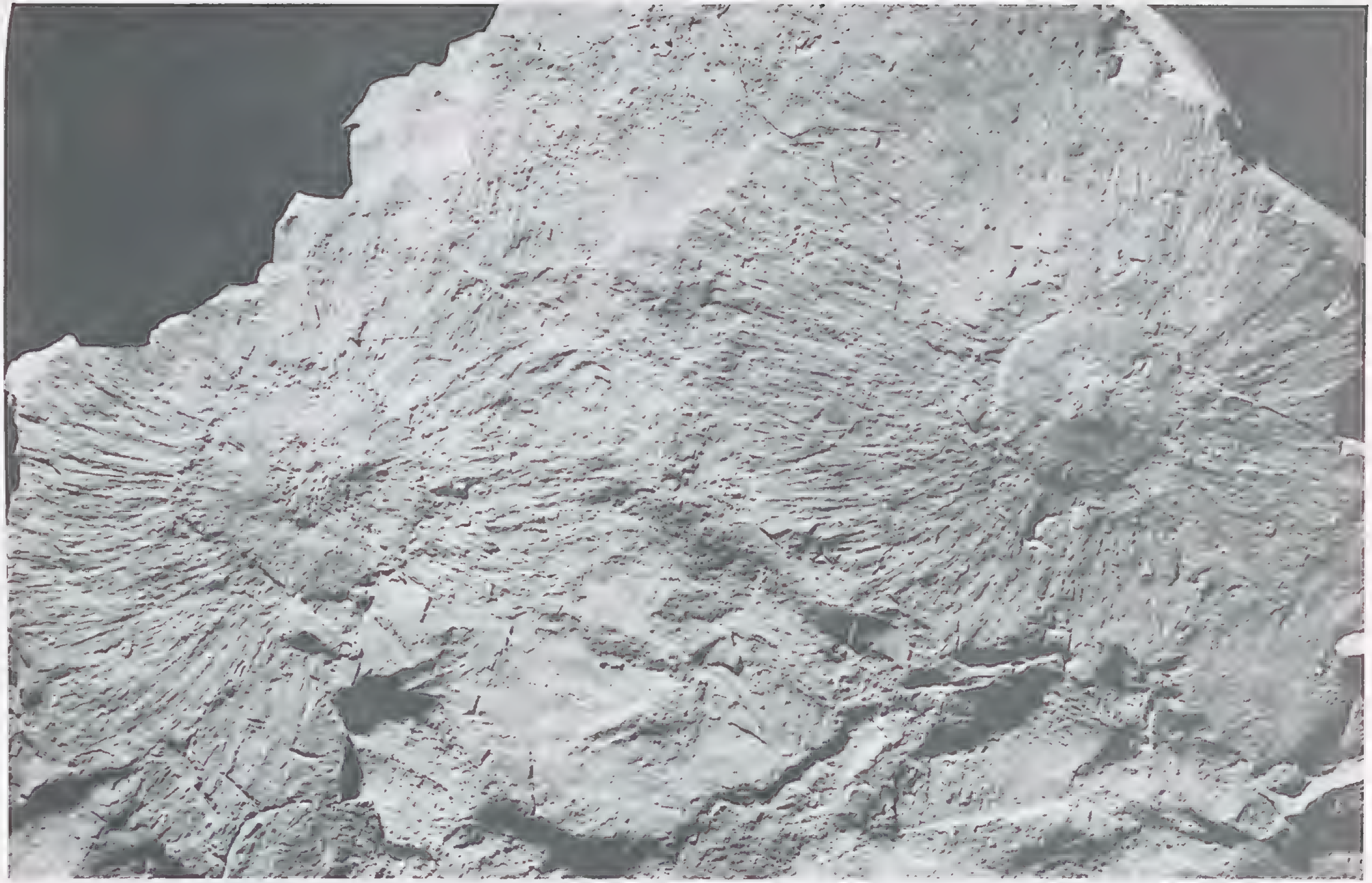

Figure 9. *Cylomeia capillamentum* sp. nov. Specimen AMF 60890. Approx. ½ natural size.

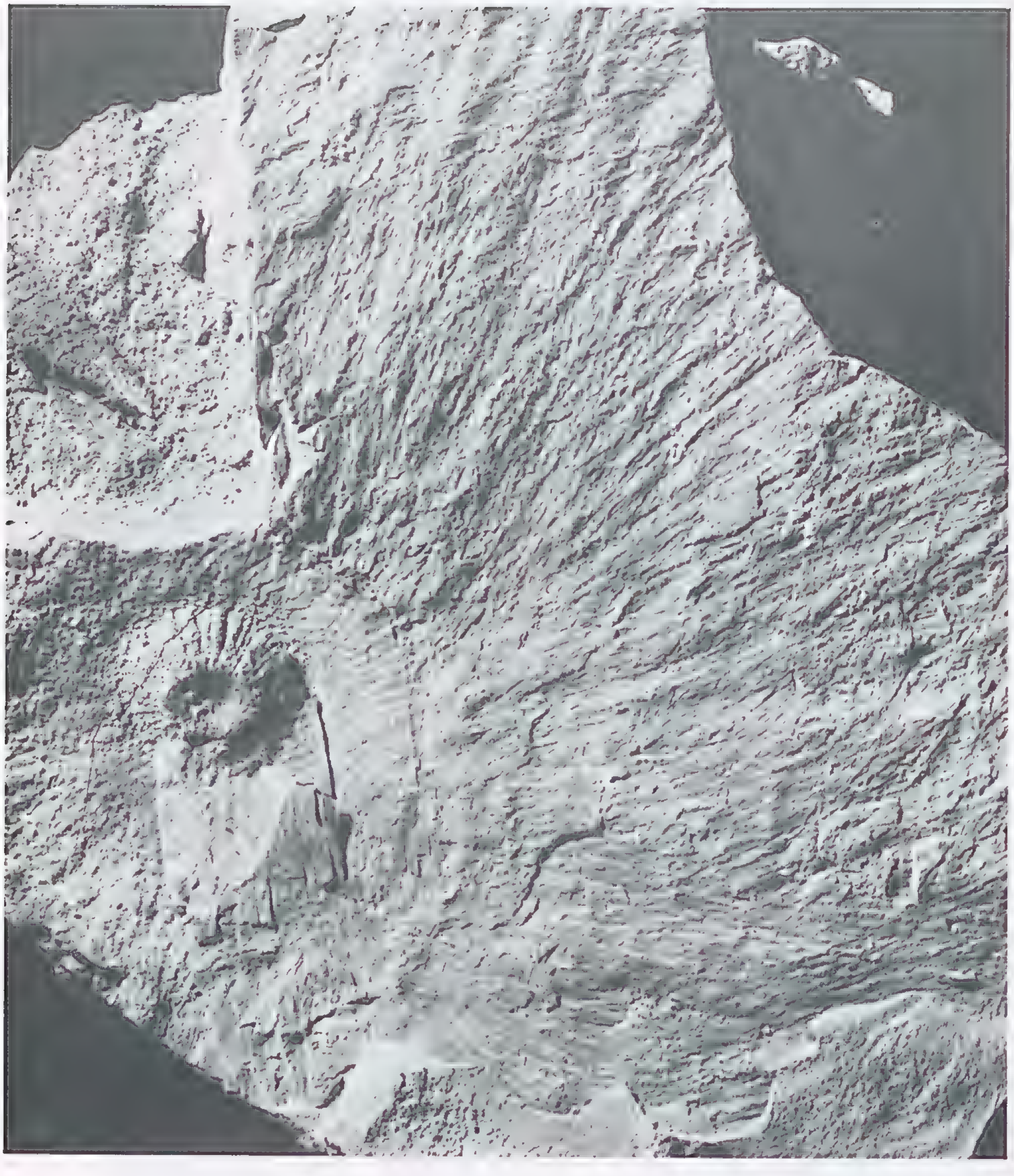

Figure 10. *Cylomeia capillamentum* sp. nov. Specimen AMF 60891. Approx. natural size. Cone *Cylostrobus capillamentum* sp. nov. at centre of whorl of hair-like leaves.

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# FUNCTIONAL MORPHOLOGY AND EVOLUTION IN THE TRIDACNIDAE (MOLLUSCA: BIVALVIA: CARDIACEA)

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## SUMMARY

The Tridacnidae are a family of the Cardiacea in which the byssal apparatus has been retained and hypertrophied in connection with obligate life on the surface of Indo-West Pacific coral reefs. The greatly enlarged siphons occupy the entire upper surface, their inner marginal folds housing enormous populations of dinoflagellate symbionts (*Symbiodinium microadriaticum* Freudenthal) exposing them to high light intensities. The umbones are displaced on to the under side alongside the byssal gape.

The least specialized species *(T. maxima* and *T. squamosa)* retain byssal attachment throughout life. On the under side intimate contact is maintained with the irregular substrate by adventitious secretion of shell around the byssal gape and by a grinding action probably assisted by chemical activity by way of the enlarged middle folds of the mantle margins. This penetration is further developed in the smaller *T. crocea* which bores into coral rock, umbonal side foremost, by this probable combination of mechanical and chemical means.

In the "giant" species, *T. gigas* and *T. derasa*, the byssal apparatus atrophies after a certain size is attained, the byssal gape closing with reduction of the mantle folds. Subsequently the unattached animals maintain themselves solely by their great weight. Adaptation here involves increase in size with the much greater number of algae that can be maintained.

*Hippopus* differs in the more globular and smoother adult shell and by retention of the siphons within the valve margins. The final habitat is on the lee of reefs, frequently on sand, with initial attachment probably on the seaward side, then early freedom and subsequent rolling over the reef surface. The globular shell represents a self righting mechanism.

Knowledge about the significance of the zooxanthellae — certainly the major food source — is reviewed and the probable course of evolution in the Tridacnidae with acquisition of the symbionts, possibly from hermatypic corals, surveyed. The Tridacnidae appear to have separated from the other Cardiacea about the beginning of the Caenozoic, possibly filling the niche left vacant when the bivalve rudists (Hippuritacea) became extinct.

Records of The Australian Museum, 1980, **Vol. 33 No. 17**, 735-777, Figures 1-29.

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## INTRODUCTION

Apart from the corals, the bivalve Tridacnidae are the most characteristic, as they are frequently the most striking, members of the fauna of Indo-West Pacific coral reefs. To look down upon their opened valves is to view the upward directed and vastly hypertrophied siphons which, richly pigmented, are continually exposed even to the strongest light (Fig. 1). Retaining their original function, the siphons have altered in size and in position so as to house and expose vast populations of the dinoflagellate symbionts or zooxanthellae which have become a major if not *the* major source of nutrition. Unique in this respect the Tridacnidae are yet related to the superficially burrowing Cardiidae and are included with that family and the Hemidonacidae in the superfamily Cardiacea. The possible course of their evolution, involving intimate association with hermatypic corals, is discussed later. After early post-larval freedom, the modern species, five species of *Tridacna* and *Hippopus hippopus,* become immobile to be invariably byssally attached in early life. Later the two "giant" species, *T. derasa* and *T. gigas,* and *H. hippopus* lose attachment although remaining immobile.

## TRIDACNID FORM

As already personally described (Yonge, 1936, 1953a, 1974, 1975) and as indicated in Figs. 2 and 29, the enlargement and consequent extension of the siphons along the entire upper surface involves (in phylogeny but *not* in ontogeny) an anti-clockwise rotation in the sagittal plane of the mantle/shell in relation to the viscero-pedal mass. The latter is effectively unaltered, foot and byssal apparatus mid-ventrally situated, in necessary contact with the substrate, throughout the long period of evolutionary change. The dorsal region of the mantle, with the umbones and hinge secreted by it, moves to the underside eventually to become situated at the anterior end of the large byssal gape. In the course of this 180° rotation, the anterior adductor is lost and the anterior byssal (pedal) retractors (abr) very much reduced. The Tridacnidae thus become monomyarian in a unique manner (Yonge, 1953b) and with the greatly hypertrophied posterior byssal retractors (pbr) in close association with the single greatly enlarged adductor (ad). The visceral organs are little affected. The anus (a) moves from its customary position on the hind surface of the adductor to the upper surface so maintaining its relationship with the anteriorly displaced exhalant aperture. The line of the ctenidial axes is little changed while the visceral organs — gut, heart, gonads and greatly enlarged kidneys — and the foot, all retain their original positions (Figs. 2, 29). The nervous system, originally figured and described by Lacaze-Duthiers (1902), is typical with a cerebro-visceral ganglion on

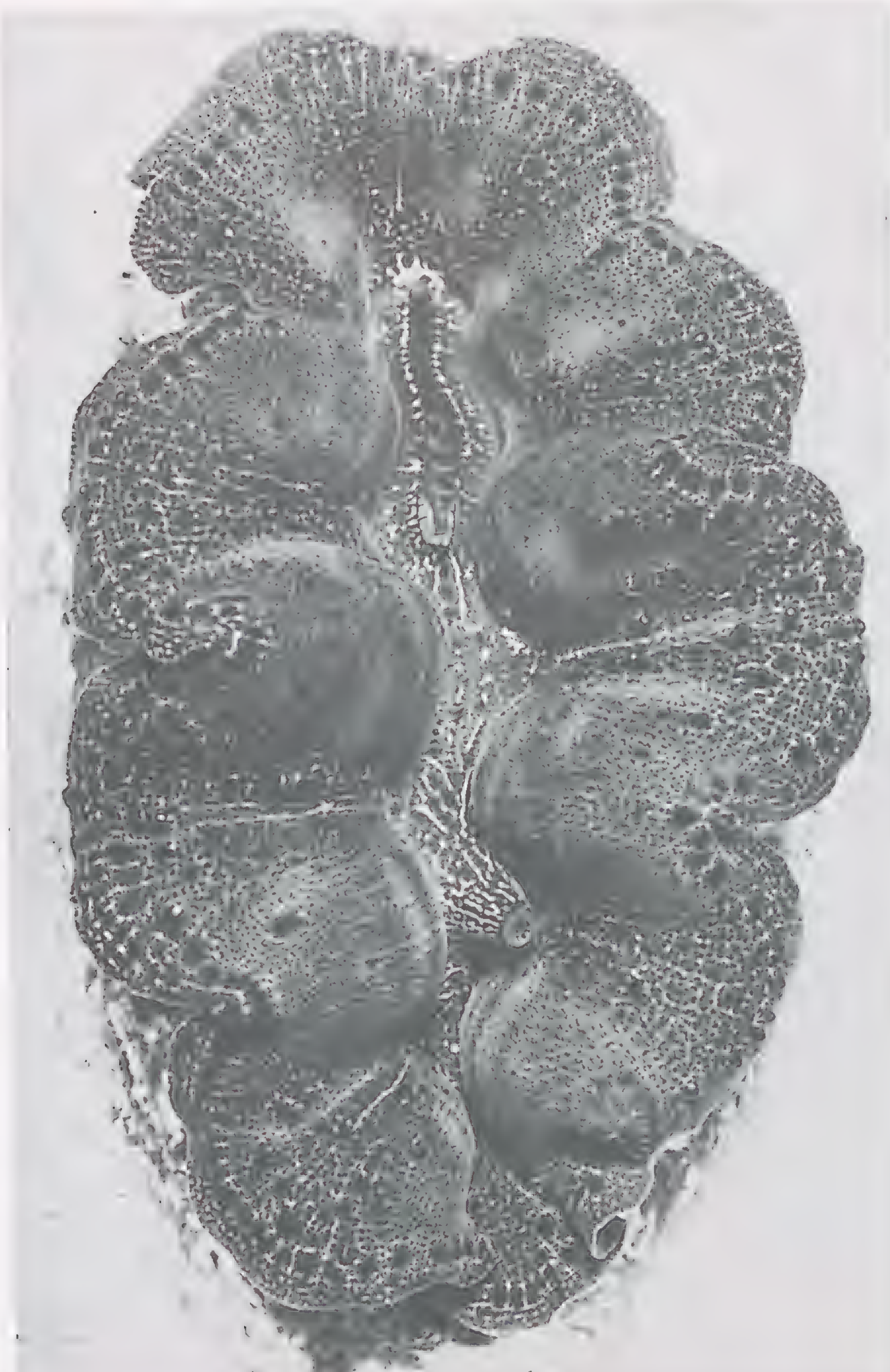

Figure 1. *Tridacna crocea*. Specimen contained in cavity within perspex viewed when siphons fully extended, elongate fully open inhalant aperture on right, tubular exhalant aperture on left, area between composed of fused inner marginal fold, peripheral areas of inner fold extensions overlapping valve margins; dark areas eyes. (Photo T. F. Goreau).

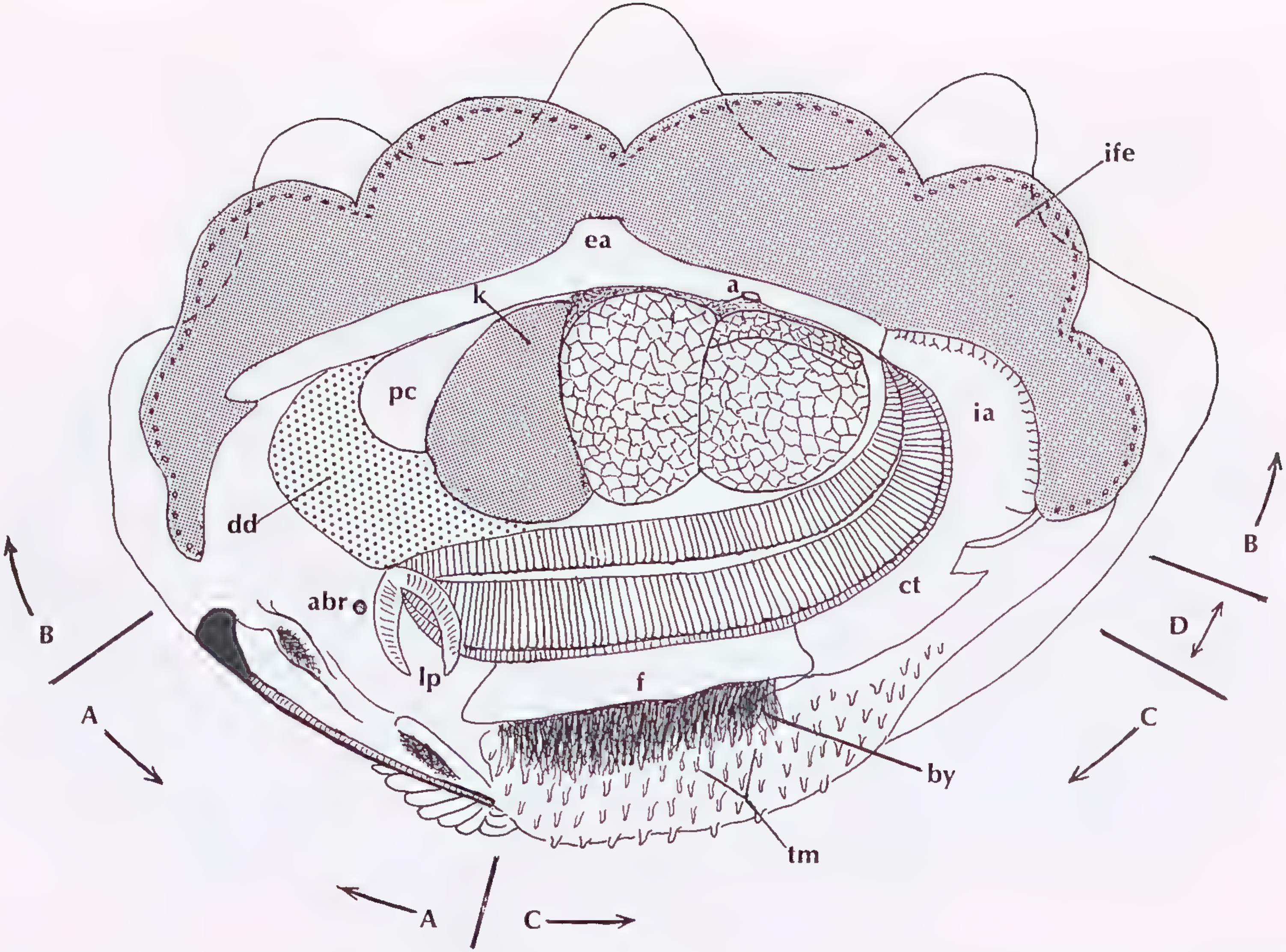

Figure 2. *T. maxima,* viewed from left after removal of valve and mantle lobe showing major organs in the mantle cavity and major peripheral areas, A—A, ligamental (cardinal) area; B—B, siphonal area; C—C, byssal gape; D, region of mantle fusion posterior to byssal gape. (Explanation of abbreviations see page 777.).

each side of the mouth, centrally placed pedal ganglia and a large fused visceral ganglion on the posterior side of the adductor. The only change from other bivalves is the anterior instead of the posterior course of the two more dorsal siphonal nerves (Fig. 3), again due to the anterior displacement of the siphons (Yonge, 1953a).

The major changes are pallial involving the orbital and adductor muscles and the shell. Forward extension of the siphons has involved corresponding movement and enlargement of the siphonal muscles (a localized region of the orbital muscles), from immediately ventral to the posterior adductor in the Cardiidae, to stretch broadly forward above the adductor along the entire upper surface of the valves (Fig. 4).

In relation to difference in habit, the shell is more elongate than in the Cardiidae while the hinge region is inevitably modified. Dentition in the Cardiidae, e.g. the common cockle, *Cerastoderma edule,* consists of central cardinal teeth below the umbones with very symmetrically sited anterior and posterior laterals. On the right valve the cardinal area consists of a deep socket with teeth on either side, in lateral areas teeth are situated above and below the sockets. The mirror image prevails in the left valve, major teeth being flanked by sockets. The ligament possesses well developed inner (fibrillar) and posterior outer (lamellar) layers with a very short anterior outer layer extending back under the inner layer — a typical opisthodetic condition.[1]

Due to rotation of the mantle/shell, in the Tridacnidae the originally anterior (now, in relation to the viscero-pedal mass, posterior) end of the hinge region at the umbones forms the anterior boundary of the byssal gape (Figs. 2, 5). The anterior lateral teeth are lost while the cardinal area is displaced ("posteriorly" in relation to the mantle/shell but "anteriorly" in respect of the viscero-pedal mass). The cardinal teeth (cth) are reduced to a single very similar tooth and socket in each valve, the tooth on the right fitting into a deep socket below that on the left. All three ligamental layers are long; the posterior outer (Fig. 15, pol) widening out and then stretching anteriorly (in relation to the mantle/shell) and topographically below the thick inner layer (il) secreted by the mantle isthmus. The anterior outer layer (aol) is much longer than in *C. edule*. The entire hinge region has moved posteriorly in relation to the umbones but the ligament is long and powerful.

The extent of the various pallial regions after rotation is shown in Fig. 2. Of the total periphery about 14% is occupied by (A) the ligamental region (mantle isthmus with epithelia secreting outer ligament layers), the remainder, consisting of the mantle lobes, being made up (B) of siphons 60% (compared with only 13% in *C. edule*), (C) byssal gape some 20% with the short extent of pallial fusion (D) between this and the siphons accounting for the remaining 6%.

As in all Bivalvia, the lobes are bordered by three folds (a fourth in a few superfamilies is concerned with directing the pseudofaecal stream). They are supremely important. The outer, as in all shelled Mollusca, is secretory forming the outer calcareous layer of the valves on its outer surface and the superficial periostracal layer in a groove usually at the base of the inner surface. The other folds are largely confined to the Bivalvia. The inner one is muscular and controls inflow and outflow of the water current created by the hypertrophied ctenidia. The middle fold is largely sensory with tentacles and sometimes eyes; this region is now in closest contact with the environment, it functionally replaces the enclosed and so atrophied head region.

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[1] A more detailed description of these ligaments will be given in a projected survey of the superfamily Cardiacea.

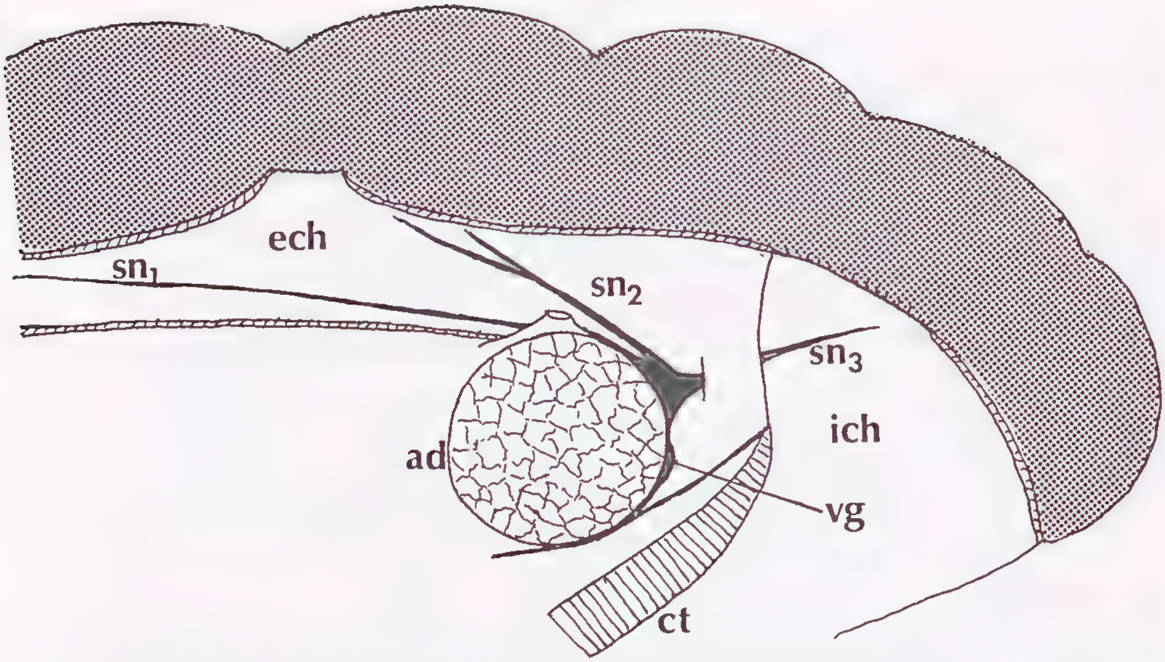

Figure 3. Modification in direction of siphonal nerves ($sn_{1-3}$) in Tridacnidae due to hypertrophy and anterior extension of siphons. (after Yonge, 1953a).

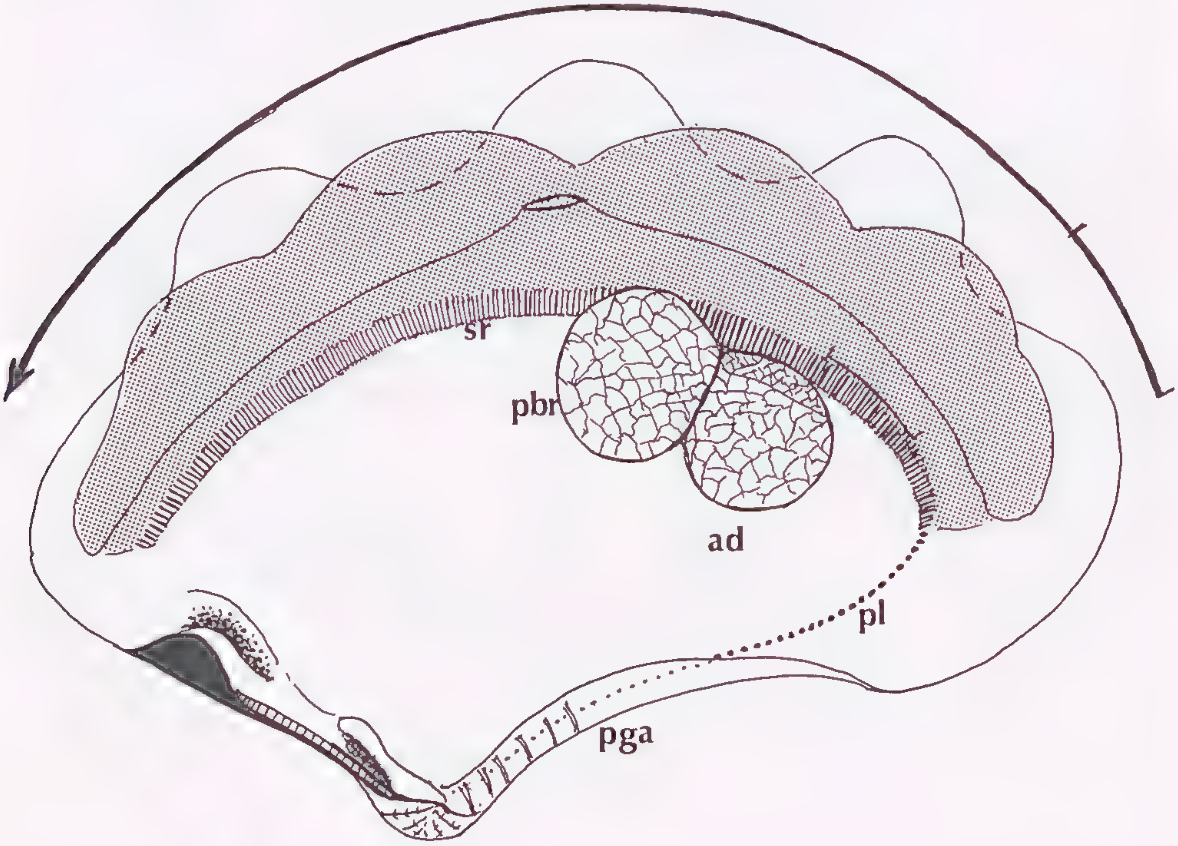

Figure 4. Anterior extension of siphonal retractors, dorsal to adductor and posterior byssal retractor, associated with anterior extension of siphons from AB to AC in the Tridacnidae.

To an extent usually consistent throughout any superfamily, the mantle lobes unite by way of these folds with fusion always beginning, both in phylogeny and ontogeny, by way of the inner folds (Yonge, 1957). Thus where siphons are present, these may be formed by fusion of the inner folds exclusively, the two siphons separate and independently mobile as in the Tellinacea (Type A), by union of inner and middle folds forming fused siphons as in the Veneracea (Type B), or with the further addition of the outer folds and so incorporating the periostracal grooves to produce the periostracally covered siphons of the often deep burrowing Myacea, Mactracea and Saxicavacea (Type C). In the Cardiacea, however, another condition prevails, not recognized when these types were described (Yonge, 1957). Here formation of the siphons involves the inner folds only but. unlike the Tellinacea, the two are united while the inner folds bear the sense organs, particularly eyes, usually carried on the middle folds. These, though present, are greatly reduced in this region. Such siphons, present in all Cardiacea but greatly hypertrophied in the Tridacnidae, are here designated Type A+.

The effect of rotation of the mantle/shell in the Tridacnidae is to separate the originally closely united siphons, the inhalant opening (ia) pulled out to form an elongate slit with the rounded exhalant aperture (ea) situated on the summit of a tubular extension in the middle of the upper surface (Figs. 1, 2). Moreover the function of the marginal folds is widely different on upper and under surfaces[1]. On the former they are modified for housing and exposure to light of the contained zooxanthellae, on the latter, around the margins of the byssal gape, for maintenance of close contact with the usually very irregular surface of the rocky substrate. No other bivalves have taken such advantage of the potentialities latent in the possession of these marginal folds in the course of adaptation to the needs of a new (and here a unique) mode of life. We return to this subject later.

## DEVELOPMENT

The Tridacnidae are all protandric hermaphrodites, the process of spawning in *T. crocea*, *T. "serrifera" (T. maxima?)* and *H. hippopus* being described by Wada (1952, 1965). The veliger larvae and the pediveligers into which these change on settlement are stated not to contain zooxanthellae (LaBarbera, 1974, 1975). Jameson (1976) reports settlement of *T. crocea*, *T. maxima* and *H. hippopus* as occurring respectively at 12, 11 and 9 days after fertilization, all of them around 200 μm long. He reports the first appearance of zooxanthellae as occurring in settled animals at respectively 19-25, 21-40 and 25-27 days after fertilization. Beyond stating that they appear in the mantle, Jameson gives no account of precisely where they first appear or of how they spread although he did observe a striking increase in the rate of growth beginning at the time of first infection. It is also unknown at what stage in the *algal life history* these infect young tridacnids. This could be by way of the non-motile stages often expelled, apparently intact, by stressed corals (Yonge & Nicholls, 1931; Goreau, 1964) but also probably in the normal process of controlling the algal population, or alternatively by one of the swimming, dinoflagellate, stages never identified in nature but appearing in culture (Taylor, 1969).

There is no information about the manner in which what is apparently (and would be expected to be) a typical bivalve veliger and pediveliger change into the unique tridacnid form with umbo and hinge alongside the byssal gape on the under side. LaBarbera (1975) finds evidence of differential growth around the valve margins as claimed by Stasek (1962). This is to be expected, the final form being attained as rapidly as possible just as it is in the even more highly modified Teredinidae where the post-larva begins to bore into wood immediately after metamorphosis (Sigerfoos, 1908; Turner, 1966). There has never been any suggestion by this writer that, as Stasek and LaBarbera appear to think, there is recapitulated in development the course of evolution involving rotation of the mantle/shell in relation to the viscero-pedal mass (as impossible here as the corresponding sequence of events would be in the Teredinidae). The course of post-larval development involving infection by zooxanthellae and their later spread in the siphons and elsewhere requires detailed study. It would also be most illuminating to follow the later course of development should infection by zooxanthellae be prevented as it so easily could be.

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[1] Reference will now be made exclusively to *upper* and *under* surfaces. This avoids the use of dorsal and ventral and so the conflict between those who regard the umbo and hinge as unalterably dorsal and those (including, as will be apparent, the writer), who consider that throughout the Bivalvia where the foot is retained this, with the byssus, is always mid-ventral, unalterably associated with the substrate whatever the effect this may have on the position of the umbones.

Little is known about the growth and habits prior to secure byssal attachment which occurs in all species whether it is maintained throughout life or not. Young *T. crocea* up to 5 mm long were personally observed moving about on rock surfaces by means of the slender foot and attaching byssally from time to time within sheltered areas such as empty barnacle shells (Yonge, 1936). In habit they resembled young *Mytilis edulis,* climbing the sides of glass aquaria in the same manner. The age of these animals was uncertain (in structure apart from the extruded and active foot, they resemble adults) but Hamner and Jones (1977) found small boring individuals of this species in October (in the same region) which they thought had settled early that year and so would be over 6 months old. There is obviously a period of freedom after the adult form is attained and before byssal attachment becomes permanent although with the differing eventual consequences described below. This period of pedal freedom will enable the animal to search the environment for a suitable horizontal surface where it can settle with the siphons facing upward. This is the initial essential need.

However this site of attachment may not be final. Recently attached animals will inevitably be dislodged by heavy seas and possibly some animals may attach and re-attach several times before finding a satisfactory site. McMichael (1974) made most interesting observations on changes over a three year period in the population of *T. maxima* in an area of some 450 square metres on One Tree Island (Capricorn Group, Great Barrier Reef). Initially 359 animals were counted, similar counts yielded 345 animals two years later and 374 the year after that. Losses could largely have been due to natural death or to predation although some small animals might have moved out and some larger ones been dislodged and carried out by water movements. Of the recorded incomers the smallest ones could have settled there directly from the plankton or have crawled in after settlement. This could not have been true of incomers between 80 and 200 mm long (36 in one year and 28 in the other). While a few might have been overlooked in earlier counts, the majority were presumably carried in by heavy seas after these had dislodged them. Numbers are great enough at least to indicate the possibility that up to a considerable size these byssally attached tridacnids may be carried to new sites where, if the substrate is suitable, they can re-attach, although the process must be rapid if predation is to be avoided. As noted later, this passive transport of sizeable animals appears to be the normal state of affairs in *H. hippopus* although the final habitat of this species is often on sand where no byssally attached tridacnid could live.

## DISTRIBUTION AND HABITAT

The species of the Tridacnidae, five of *Tridacna* and *Hippopus hippopus* (Linnaeus 1758), inhabit areas of varying extent within the tropical Indo-Pacific (for taxonomic details and maps of distribution see Rosewater, 1965). They invariably occur in association with coral reefs, requiring much the same range of temperature as do most hermatypic corals. Their need for light is even more demanding, for instance at Palau (Hardy & Hardy, 1969) in the clearest water on the seaward side of reefs tridacnids do not occur below depths of about 20 metres while in more turbid lagoon waters they are confined to areas of only half this depth. The creation, therefore, by coral growth of extensive shallow water areas provides them with their required habitat including wide areas of dead coral which supplies the hard substrate needed for initial settlement and often for permanent colonization. From the living coral possibly also may come the zooxanthellae which, as noted above, are not acquired until after settlement.

All species are initially attached by a massive byssus. This is clearly the primitive tridacnid habit with subsequent immobile "freedom" in certain species a secondary condition. Attachment is retained throughout life in *T. maxima* (Röding 1798), *T. squamosa* Lamarck 1819, and in the boring *T. crocea* Lamarck 1819, these three constituting what Rosewater designates the subgenus *Chametrachea*.

The two first (with the most primitive habit) have the widest distribution extending from the western extremities of the tropical Indian Ocean (to the north including the Red Sea) to the central south Pacific. Presumably they possess the greatest range of breeding temperatures while possibly their larvae spend the longest periods in the plankton. They are also probably the oldest species. In both, the siphons have a bewildering range of colours (see Rosewater, 1965), with hardly two patterns the same[1]. Shell lengths of over 300 mm are attained but *T. squamosa* is broader with more rounded marginal interdigitations of the shell valves and more centrally placed umbones. The projecting scales, present in rows on the ridges on the outer surface of the valves in both, are more pronounced in *T. squamosa* which is usually attached to a firm surface whereas *T. maxima* tends to settle upon, or perhaps make its post-larval way by crawling on to, coral rubble. In both, the broad undersurface is extensively and most firmly attached by byssal threads which appear somewhat more gelatinous in *T. squamosa*. By contractions of the large posterior retractors the shell is pulled firmly down often, particularly in *T. maxima*, penetrating into the substrate especially where this is less coherent. An extreme instance is that of an individual 254 mm long by 190 mm high which was found embedded to a depth of some 130 mm in rubble. The surface of the valves was worn smooth to this height, above this scales protruded. As described below for *T. crocea*, this boring is almost certainly assisted by chemical (probably chelating) action with the certainly accompanying grinding action produced, again as in *T. crocea* (Fig. 18) by alternate contractions of right and left posterior byssal retractors. Where animals are more superficially sited (or the rock surface more impenetrable) protection of the byssal opening is ensured by formation of the byssal "funnels" described below. The final effect in all cases is extremely secure and intimate attachment; it is most difficult to detach well grown specimens of these species and impossible for predators to enter.

*T. maxima* is the commoner with a somewhat wider distribution. It is the only tridacnid found throughout the Gulf of Eilat at the head of the Red Sea (Goreau, Goreau & Yonge, 1973) and, diagonally across the tropical Indo-Pacific, in the Tuamotus where Salvat (1969, 1971) found it in the closed atolls at densities up to 63 large individuals per square metre with an estimated weight per hectare of 37 tons of shell, with 7 tons of contained tissues. On One Tree Island, McMichael estimated a total population (of *T. maxima* alone) of over 2 million with estimated growth to lengths of around 240 mm in

[1] As shown by Kawaguti (1966), pigmentation is due to iridophores. However where tridacnids live in shade, or are subjected to such conditions, the siphons become extremely pale indicating that these structures as well as the zooxanthellae are affected by lack of light.

somewhat over forty years.

The boring habit is developed to the full in the small *T. crocea* which penetrates solid coral rock with the valve margins flush with its surface over which the richly pigmented (usually blue) siphons extend as a conspicuous scalloped sheet of tissue (Fig. 1.) This species is restricted to the central Indo-Pacific but within this still very extensive area it is usually the commonest and certainly the most successful species, this due to the great protection afforded by boring. Hamner and Jones (1976) provide impressive data about its density with numbers "regularly exceeding 100 clams/$m_2$ with notable effects on erosion and sediment production".

In the remaining species, the "giant clams" *T. gigas* (Linnaeus 1758) and *T. derasa* (Röding 1798), attachment is lost after a certain age when the byssal gland atrophies and the gape closes. The animals subsequently maintain themselves in an upright position solely by virtue of their great weight. Large individuals of *T. maximus* were encountered with a reduced byssal opening suggesting that its closure, with reduction and atrophy of foot and byssal gland, would be the consequence of further increase in size and so inevitably occur, after a certain age, in any large species of tridacnid.

Both are restricted to much the same regions in the Central Indo-Pacific from the west coast of Sumatra to Fiji (Rosewater, 1965). *T. gigas* is the largest bivalve ever evolved, the shell reaching recorded lengths of 1370 mm. It has resemblances to *T. squamosa* but has no scales on the valves. *T. derasa* is smaller not exceeding lengths of around 510 mm and easy to distinguish owing to the much lower radial sculpture. Both occur in shallow water and may be partially exposed at low tide. They would seem to settle in relatively sheltered areas where they are unlikely to be displaced while still attached; after this they become too massive to be moved. The two species doubtless have distinct ecological needs but these have never been determined.

The horse-hoof clam, *H. hippopus,* is easily distinguished by its more spherical form, very closely interlocking valves and enclosure of the siphons entirely within the valve margins. It has much the same distribution as those of the two giant tridacnids and like them loses attachment. But it does so at a much earlier age to be then rolled across the reef surface sometimes to remain on this but frequently coming to final rest on sandy substrates in the lee where it may often form the most conspicuous member of the fauna (Fig. 22).

## ADAPTATIONS

The major, and unique, adaptation in the Tridacnidae is the modification, with their accompanying great enlargement, of the siphons for housing and exposure to light of the symbiotic zooxanthellae. This involves enormous hypertrophy of the inner mantle fold on the upper surface. But during attachment, i.e. throughout life in permanently attached species, the middle mantle folds are no less significantly modified on the *under* surface. Conditions on both surfaces are shown in Fig. 6. In consequence there is great dissimilarity in the position and width of attachment of the pallial (orbicular) muscles on upper and under surfaces. As shown in Fig. 4, on the former the siphonal retractors (modified and hypertrophied orbicular muscles) are broad and attached well within the margin of the valves whereas on the under side the pallial muscles form only a thin line of attachment just within the rounded margin of the byssal gape.

Description now follows of these adaptations and of their significance in the life of the animals together with that of other adaptations involving boring, increased size and loss of attachment and final freedom in *Hippopus* from dependence on a hard substrate.

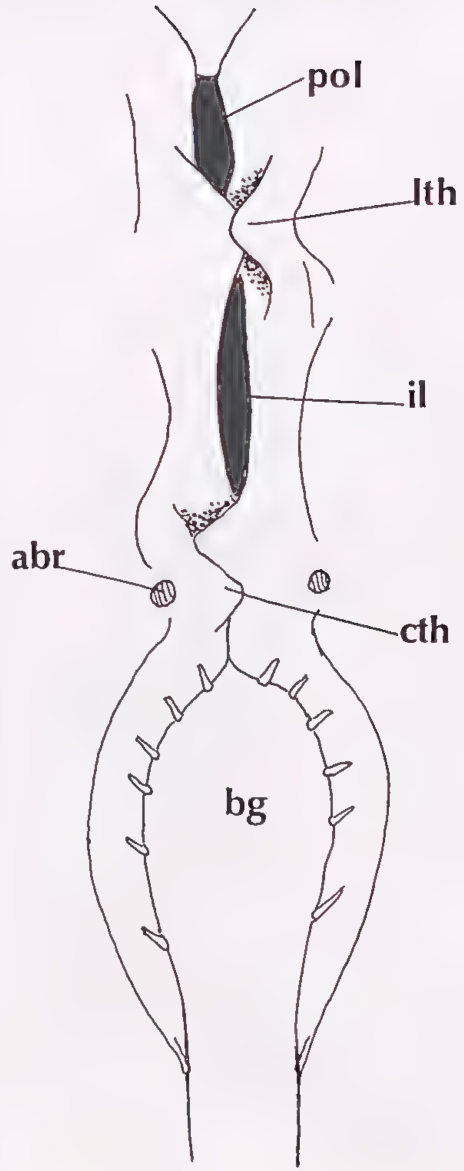

Figure 5. *T. squamosa*, byssal gape and hinge region viewed from within.

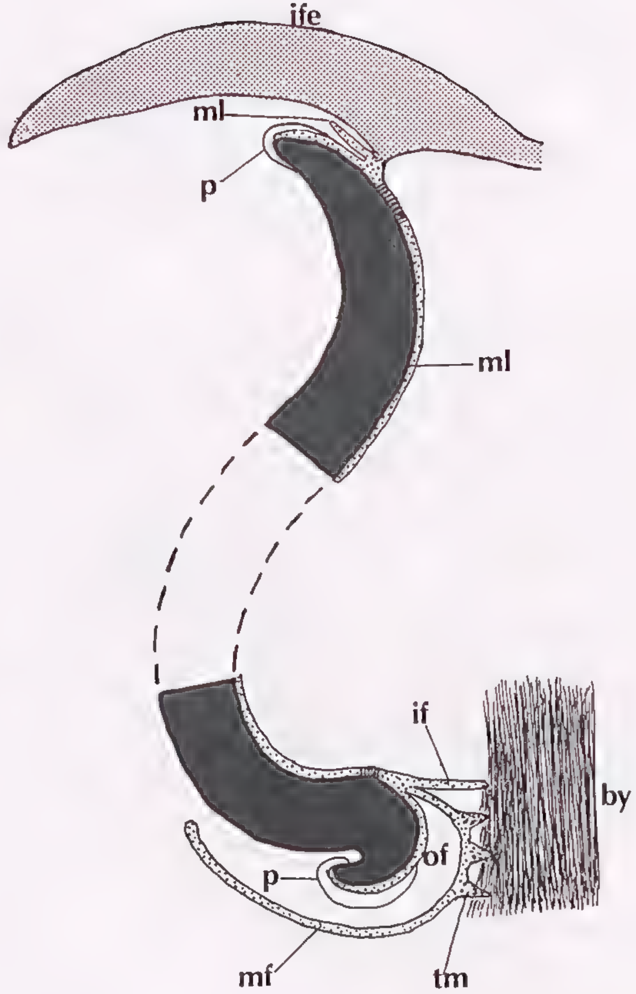

Figure 6. Mantle margins in *Tridacna*, semi-diagrammatic representation showing differences in modification on upper and lower surfaces, inner folds hypertrophied on former and middle folds on latter.

(a) Permanently Attached Species (*T. maxima, T. squamosa, T. crocea*)

**Upper Surface:** the richly pigmented siphons extend in a series of deep, slightly overlapping lobes well beyond the margin of the valves to form a flat platform. The *entire exposed surface* (i.e. all shown extended in Fig. 1) consists of the greatly hypertrophied inner marginal folds. These are extended laterally when the valves open, upward when they are closed, to form what are here described as the inner marginal fold extensions (ife) which surround the entire siphonal area (Figs. 1, 2) uniting centrally (fif) between the two openings (i.e. Type A+siphons). This region is shown, following contraction due to fixation, in the transverse section of a very small *T. crocea* (ca. 1 cm long) in Fig. 7.

These folds are everywhere penetrated by branches of the siphonal muscles (sr) responsible for their withdrawal and by the blood sinuses (bs), pressure in which causes their extension when the valves separate. These are also the site of great numbers of zooxanthellae and the means of their eventual transport into the visceral mass. On one side of the figure an eye (ey) has been sectioned. These were earlier described (Yonge, 1936) as "hyaline organs" because although they had a somewhat dumb-bell shaped lens there was no evidence of either retina or nerves. They were regarded as vestigial eyes, the lens retained for better conveyance of light deep into the tissue for the benefit of the zooxanthellae[1]. But more recently, using the electron microscope, Stasek (1966) and in more detail, Kawaguti and Mabuchi (1969) have identified both retinal cells and nerves with Frankboner (1979) finding them totally composed of retinal cells. It appears that these organs, which occur in a more or less regular row near the margins but are also scattered irregularly elsewhere, are responsible for initiating the reflex movements that culminate in sudden expulsions of water through the exhalant siphon. Eyes are certainly present on the tips of the tentacles on the inner fold around the siphons in many, possibly all, species of Cardiidae; on the other hand there are no eyes in *Hippopus*.

The middle folds (Figs. 6, 7, mf) although always present, are never visible on the upper surface. In the section they are greatly contracted following fixation appearing very small both in comparison to the immense inner folds on the one side and the elongated outer folds (of) on the other. When examined in life after removal of the valves in *T. maxima* (Fig. 8) they are revealed as being delicately pigmented with iridescent spots of gold on the inner surface. A few zooxanthellae are contained within the tissues indicating some exposure to light but the sensory functions usually possessed by these folds are absent.

The outer, secretory, fold (Figs. 6, 7, 8, of) is equally obscured in life. It is colourless and without zooxanthellae. The periostracal groove (pg) which in other bivalves is situated between the bases of middle and outer folds, here runs along the inner face of the outer fold some two thirds of the distance from the tip. There can be no question here — as there has been in other bivalves — as to whether the groove is associated with the middle rather than the outer fold. Observed in life the marginal two thirds of the inner surface of this fold is covered with transparent periostracum continuous with the superficial covering of the shell. Within the extrapallial cavity so created the outer, prismatic layer of the valve is secreted by the outer surface of the outer fold.

The secretory activities of the outer fold co-operate with the inner fold extensions to provide the maximum possible surface area for horizontal exposure. The generative curve is thrown into a series of what Rosewater describes as interdigitating projections representing a great increase in length. This is true of all tridacnids. In a shell of *T. gigas* 36.5 cm long, the length of the curved upper surface is about 53 cm but the actual length

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[1] This may have a measure of truth; zooxanthellae are always particularly numerous immediately around them.

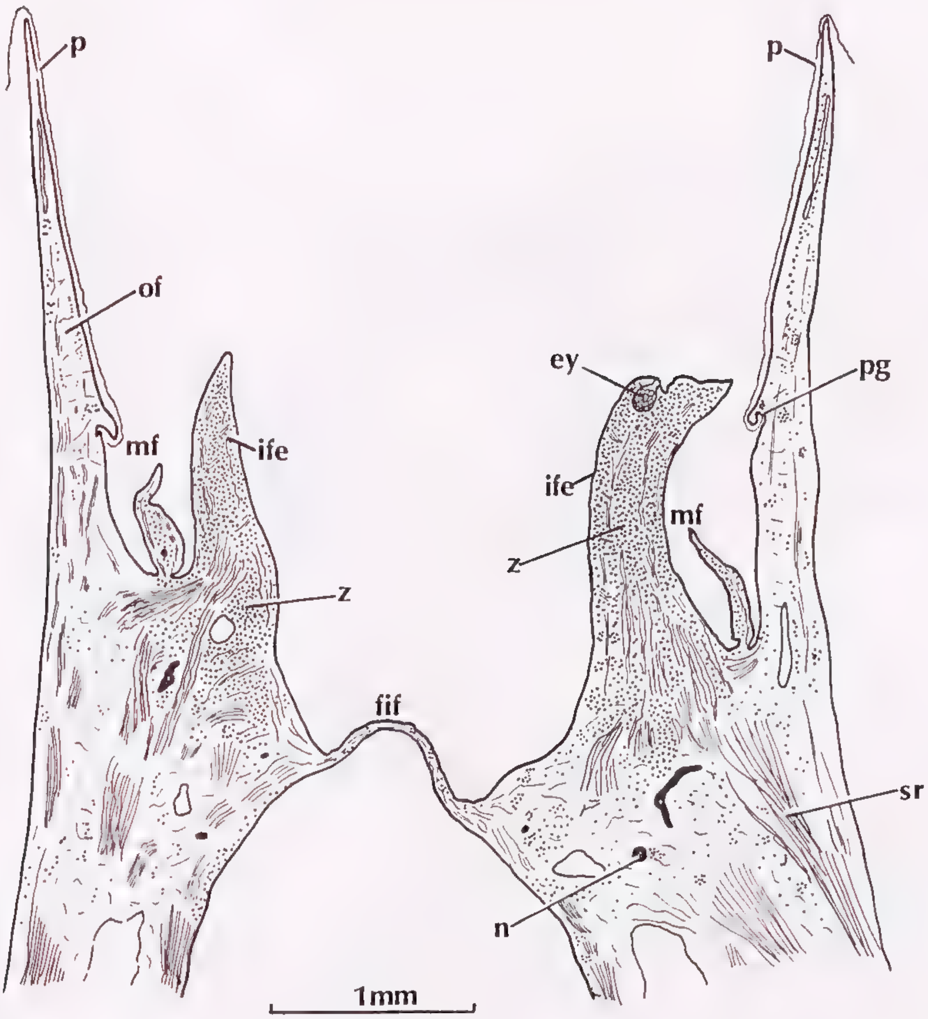

Figure 7. *T. crocea*, transverse section through middle of upper surface showing mantle lobes (much contracted).

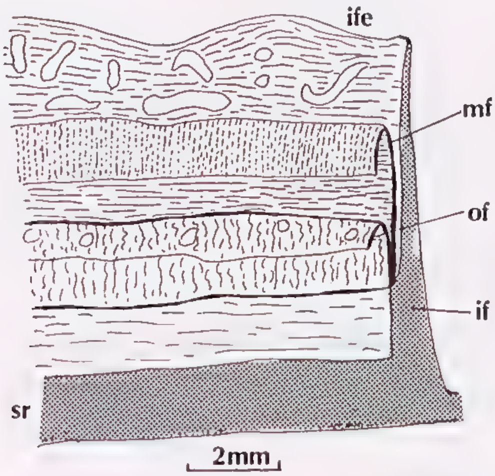

Figure 8. *T. maxima*, drawing, in life, of mantle margins on upper surface viewed from outer side after removal from shell.

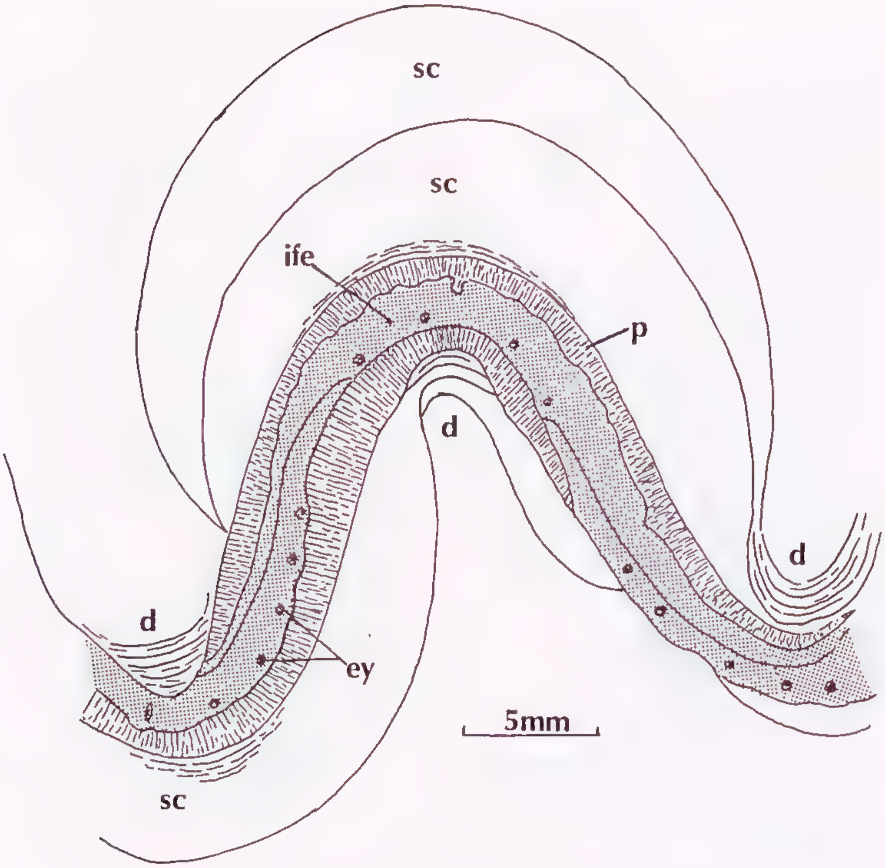

*Figure 9. T. squamosa,* region of upper surface with valves almost closed and only limited area of siphonal tissues with marginal periostracum visible; shows close interdigitation of valve margins.

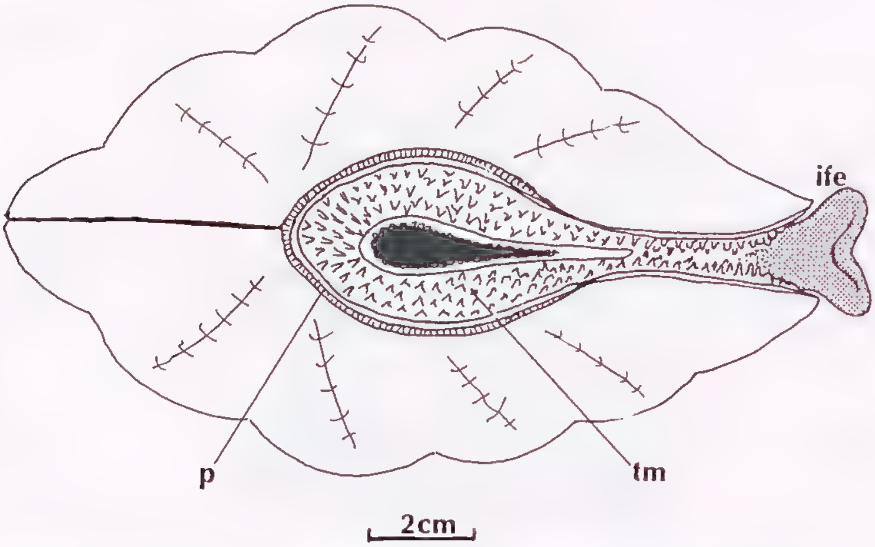

Figure 10. *T. maxima,* intact animal viewed from under surface showing byssal gape with elongate byssal mass surrounded by middle mantle folds with numerous blunt tentacles.

of the undulating margins of the valves is 85 cm. As a result of these undulations, the length of the mantle margins is increased by some 60%. This involves a corresponding increase in the length of the inner mantle folds and so in space for accommodation of additional zooxanthellae.

In these permanently attached species the deep radial grooves in each valve which correspond with the marginal depressions carry a series of projecting scales already noted as being most conspicuously developed in *T. squamosa*. These are added to periodically during growth but worn away basally where the animal grinds into the substrate. Their formation involves a series of extensions by the outer marginal folds beginning, as shown in Fig. 9, by topographically upward growth from the base of the preceding scale (this occurring obscurely beneath the overlying inner folds). Addition to the outer calcareous layer occurs within the periostracal sheet which is attached at progressively higher levels until a further burst of secretory activity produces another scale.

This process has resemblances to the formation of "shoots" in the Ostreacea but reduced growth continues between successive bursts in the Tridacnidae which it does not in these oysters. The final effect is the formation of a broad shell platform on which the expanded siphonal margins are supported.

What has to be said about the siphonal openings covers all species. The extended inhalant aperture (attaining 1/3 the length of the animal) is fringed with very short, usually branched tentacles. These are best developed posteriorly but can only act as strainers when the two sides are very close. The short exhalant tube is extremely mobile folding inward when not open. Through it is directed, with impressive force, the large volume of water that accumulates in an exhalant chamber (Fig. 2) which, due to the anti-clockwise rotation of the siphons stretches to the anterior end of the upper surface (Yonge, 1953a) forming what Stasek (1965) has very suitably termed a "suprabranchial cul-de-sac". Thus, whereas in other bivalves adduction produces the greater outflow through the inhalant opening, so aiding in the disposal of pseudofaeces, the opposite is true of the tridacnids, where pseudofaeces are of minor importance. Stasek (1965) and also McMichael (1974) claim that the water jet is directly aimed against possible predators such as an approaching fish. This is perhaps less certain but the quick muscle of which the adductor is very largely composed certainly reacts to any stimulus reaching it by way of the visual organs on the inner fold extensions. This may often be the shadows of fish which do frequently bite into the exposed siphonal tissues. These can, however, be withdrawn by contraction of the siphonal retractors without involving the adductor.

**Under Surface:** the structure of the mantle margins along the under surface in *T. maxima* is shown in Fig. 10 with a transverse section through the middle of the byssal gape of *T. crocea* in Fig. 11. The gape is of impressive size in these attached species owing to the exceptional extent of the byssus needed for securing these animals in shallow, well illuminated, but often highly agitated, waters. One example may suffice, that of a specimen of *T. maxima* 205 mm long by 115 mm broad in which the byssal opening was 50 mm long and 34 mm wide. The byssus consisted of a solid central mass about 13 mm in diameter pointing forward and with many attached strands on each side. These were securely cemented to the substrate of irregular coral rock over an area some 30 mm in diameter. Sizes of byssal gape and byssus vary widely but examination of specimens of *T. maxima* ranging in length between 135 and 240 mm revealed byssal openings of between 30 and 60 mm long and 24 and 35 mm wide. In *T. squamosa* of between 200 and 225 mm in length byssal gapes ranged in size from 45 by 15 mm to 55 by 30 mm.

The presence of so large an opening on the under side of a defenceless animal incapable of movement presents major problems. The entrance of any of a host of small

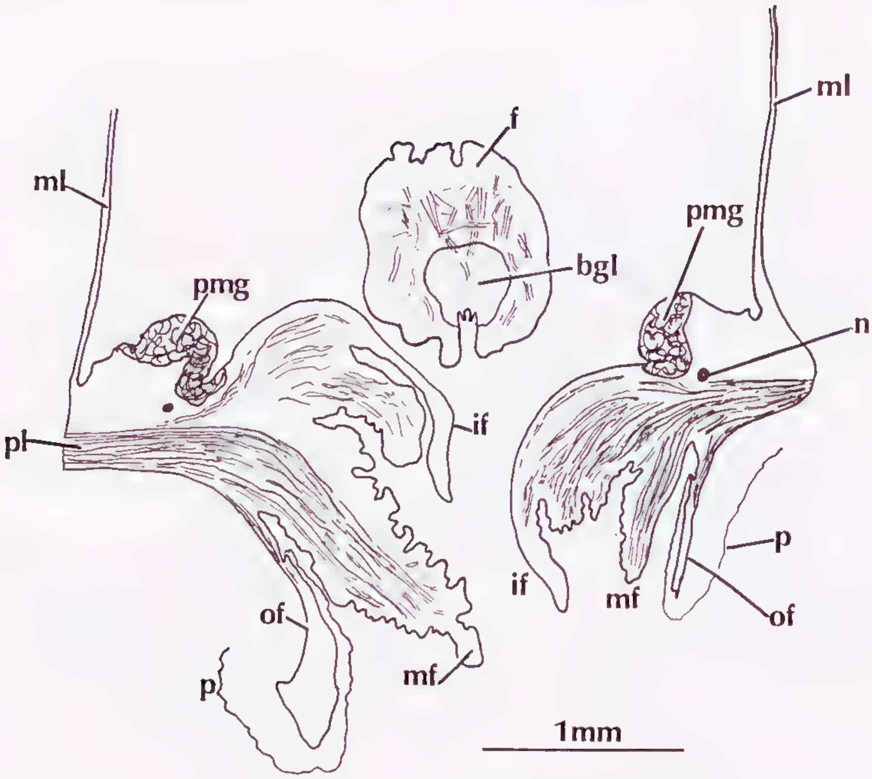

Figure 11. *T. crocea*, transverse section through middle of byssal gape cutting through foot and mantle lobes with pallial mucus glands and marginal folds showing great enlargement of middle folds.

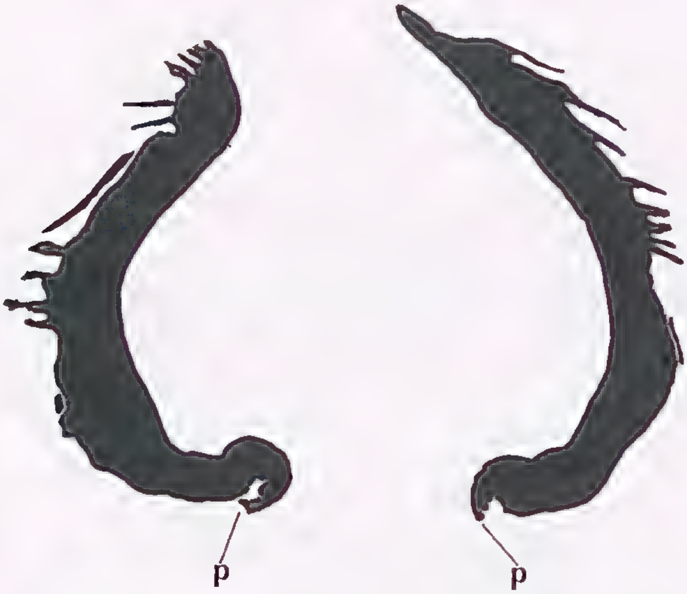

Figure 12. *T. maxima*, shell valves (somewhat separated) embedded in resin and cut transversely in middle of byssal gape, showing scales on outer surface and outward curling of shell margins round gape, due to activities of outer mantle folds.

carnivores — notably errant worms, crustaceans, gastropods and fishes — must be prevented. It is not enough merely to contract the byssal retractors because the coral substrate is usually highly irregular and openings between shell and substrate would usually be left through which such enemies could enter quickly to eat the enclosed animal. That no such spaces normally exist is due to the activities of the marginal folds around the gape.

The inner folds (Figs. 6, 10, 11) are here reduced to their customary size providing no more than a border round the opening through which the byssus emerges. It is the middle fold that is modified being greatly enlarged and extending outwards between reduced inner and attached outer folds.

As shown in Fig. 10, on the under side the middle folds emerge from below the hypertrophied inner folds, under which, on the upper surface, they are completely obscured. They lose pigmentation and enlarge greatly with the appearance of increasing numbers of conical tentacles set in irregular rows. These do not appear to be sensory but do form an elaborate meshwork through which the byssal threads pass and which possibly assist in their suitably wide planting. They also secrete mucus which may repel small invaders. Certainly the large byssal gape is occupied by byssal threads surrounded by, and marginally intermingled with, these rather fleshy tentacles (Fig. 19). As shown in Figs. 6 and 18, the distal regions of this fold do not carry tentacles but extend as a smooth sheet for some distance outside the byssal gape. This region, as we shall see, is more extensive in *T. crocea* than in *T. maxima* and *T. squamosa,* and there is clear evidence that in that species it assists, chemically, in excavating the boring. To the variable extent to which the substrate is excavated in *T. maxima* and *T. squamosa,* the distal region of the middle fold may be capable of the same activity in these species.

Starting somewhat posterior to the gape, the outer folds begin to curl outwards to secrete, around the gape, a rounded margin (Figs. 5, 6, 12) composed of many closely applied layers within the line of periostracal attachment (p). Anteriorly, i.e. in the umbonal region, periostracal attachment extends across from one valve to the other. The sides of the gape bear a series of transverse ridges (Fig. 4) increasingly widely separated posteriorly.

Such is the condition when animals are attached to a more or less flat and continuous surface. But where this is irregular, and so more frequently in *T. maxima,* adventitious shell usually consisting of alternate layers of periostracum and calcareous valve, secreted respectively by inner and outer surfaces of the outer folds, is laid down particularly around the umbonal end of the gape. The result is the formation of what may be termed a "byssal funnel" which can be of considerable size, that shown in Fig. 13 being some 20 mm high anteriorly and gradually diminishing behind. Everywhere the irregular margins conform with the irregularities of the substrate against which they are firmly pressed.

A more detailed examination of the nature of these adventitious additions to the margins of the byssal gape — so far as can be determined unique among the many, largely unrelated, byssally attached bivalves — is provided in Fig. 15 showing longitudinal median sections of a resin embedded shell of *T. maxima.* There are obviously irregularities in the formation of the funnel which involves roughly alternate layers of calcareous and periostracal secretion. As shown in Fig. 13, the overall appearance may be like that of a human lower dentition but with small molars, no canines and greatly enlarged, barely separated, incisors of varying sizes.

Although not so frequently developed, byssal funnels are also formed in *T. squamosa* (Fig. 14). In both species the funnel widens basally; thus in one specimen of *T.*

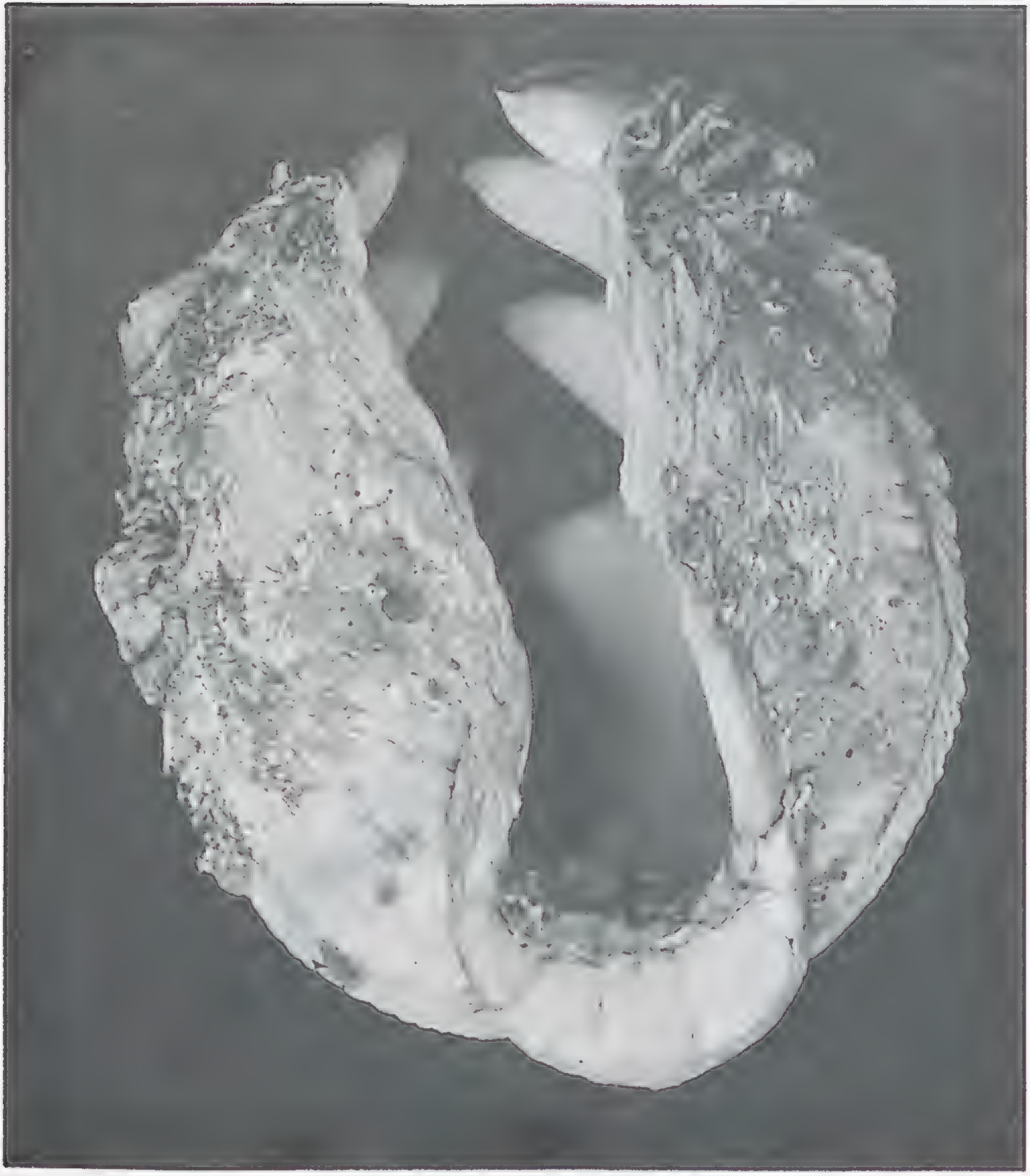

Figure 13. *T. maxima*, under view of shell valves showing byssal gape with very well developed byssal funnel around the umbonal end. (Photo A.I.M.S.)

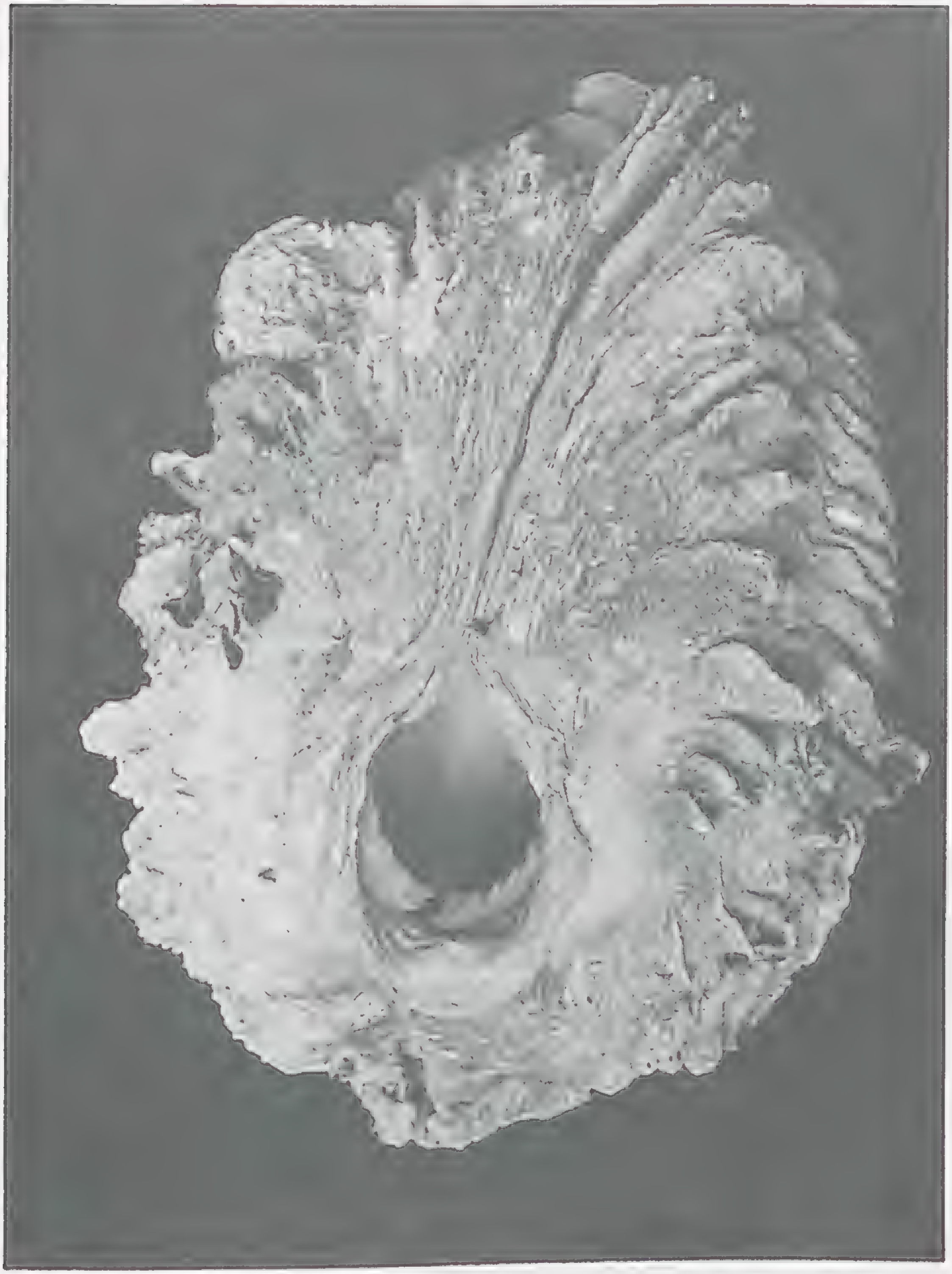

Figure 14. *T. squamosa*, similar view showing byssal gape and funnel, also prominent scales characteristc of this species. (Photo A.I.M.S.)

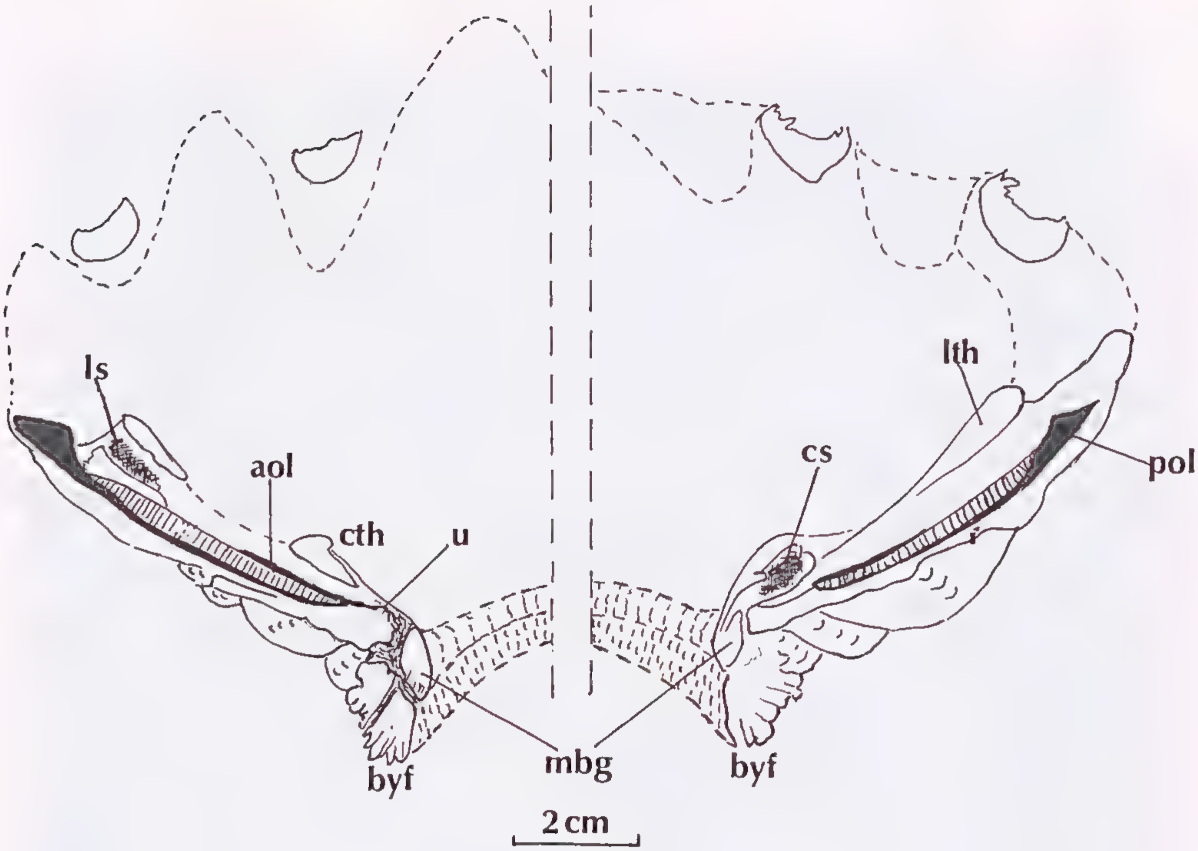

Figure 15. *T. maxima,* resin-embedded shell with large byssal funnel cut along mid-line longitudinally with halves turned to face forward, i.e. left valve on right, right valve on left. Ligament and dentition shown with large byssal funnel cut at right angles at umbonal end and seen diminishing posteriorly within resin (see broken lines). Note distinction between upper regions (mbg) formed by outward curling of margins of the byssal gape and adventitious secretion below (byf).

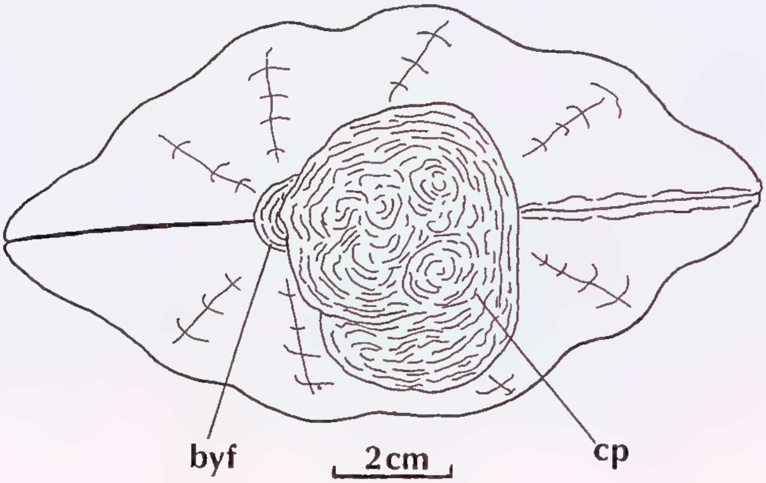

Figure 16. *T. maxima,* under view of a specimen with byssus attached to a free piece of calcareous matter forming a plug to the byssal gape.

*squamosa* the outer (lower) dimensions of the opening were 60 by 40 mm and the inner (upper) ones 35 by 28 mm. In other byssally attached bivalves (e.g. *Pinna, Pinctada, Mytilus)* the gape is extremely narrow; there is no danger of predators entering. Owing to the much greater size of the byssal mass and the irregularity of the substrate, conditions are totally different in the Tridacnidae.

The gape may, however, be closed in another manner. During 1967, when on the *De Moor* Expedition, a specimen of *T. maxima* was found which had been lying on the left side (Fig. 16). The marginal scallopings on that side were enlarged, those on the other side reduced so that the siphons were more or less horizontally extended. Survival had been possible because, as shown in Fig. 16, the gape had been closed effectively by a "plug" of some calcareous material held in place by the byssus. At the umbonal end the opening was further blocked by local secretion of a reduced byssal funnel fused to the upper surface of the plug.

Protection of the wide byssal gape by the basal tentacles on the enlarged middle mantle folds with the distal region of these folds probably assisting penetration into the substrate, together with the formation of byssal funnels by the outer folds, all represent basic adaptations. Only by such means could the Tridacnidae have successfully established themselves on the irregular — but essential, because *illuminated* — upper surface of reefs and eventually have achieved the size made potentially possible by the additional source of nutrition provided by the zooxanthellae. In *T. maxima* and *T. squamosa* this protection of the byssal gape continues to be as important as the hypertrophy of the siphons on the upper surface. In the further course of evolution it ceases to be important after a certain age in the giant species and in *H. hippopus* while in the boring *T. crocea,* now to be considered, no funnel is needed while the middle folds on the under side are further developed in connection with the boring process.

(b) Boring Species *(T. crocea).*

This is the smallest species, rarely reaching its maximum length of 150 mm. It differs in no way from *T. maxima* and *T. squamosa* on its upper surface and is even more firmly attached but needs to be considered separately because of its different mode of life with associated adaptations. It has joined company with a wide assortment of unrelated bivalves (species of Mytilacea, Myacea, Veneracea, and Saxicavacea with all species of Pholadacea and Gastrochaenacea) in the ability to bore into rock, here always of coral origin. *T. crocea,* however, is unique in penetrating by way of the under, umbonal, instead of the anterior, surface. This is a consequence of the basic tridacnid habit of extensive byssal attachment and is foreshadowed by the limited extent of downward penetration noted particularly in *T. maxima.* It involves further modification of the middle marginal folds on this side and results in a highly successful mode of life. The animals penetrate to their full depth with the broad inner fold extensions spreading widely over the rock surface and completely obliterating valves and boring below (Fig. 1). Thus from a boring with an opening 90 mm long and 15 mm wide there emerges a sheet of intense blue tissue some 105 by 55 mm in extent to provide an area of about 5775 sq.mm in which zooxanthellae are exposed to light.

The only previous, and inadequate, account of the boring process has been given by this author (Yonge, 1936), although Hamner and Jones (1976) have recently presented a wealth of data about the ubiquity of the species in shallow waters on the inner reefs of the Great Barrier and of the impressive effect its activities have on erosion. *T. crocea* probably demands relatively sheltered water for initial settlement but once established within a boring no tridacnid is so secure.

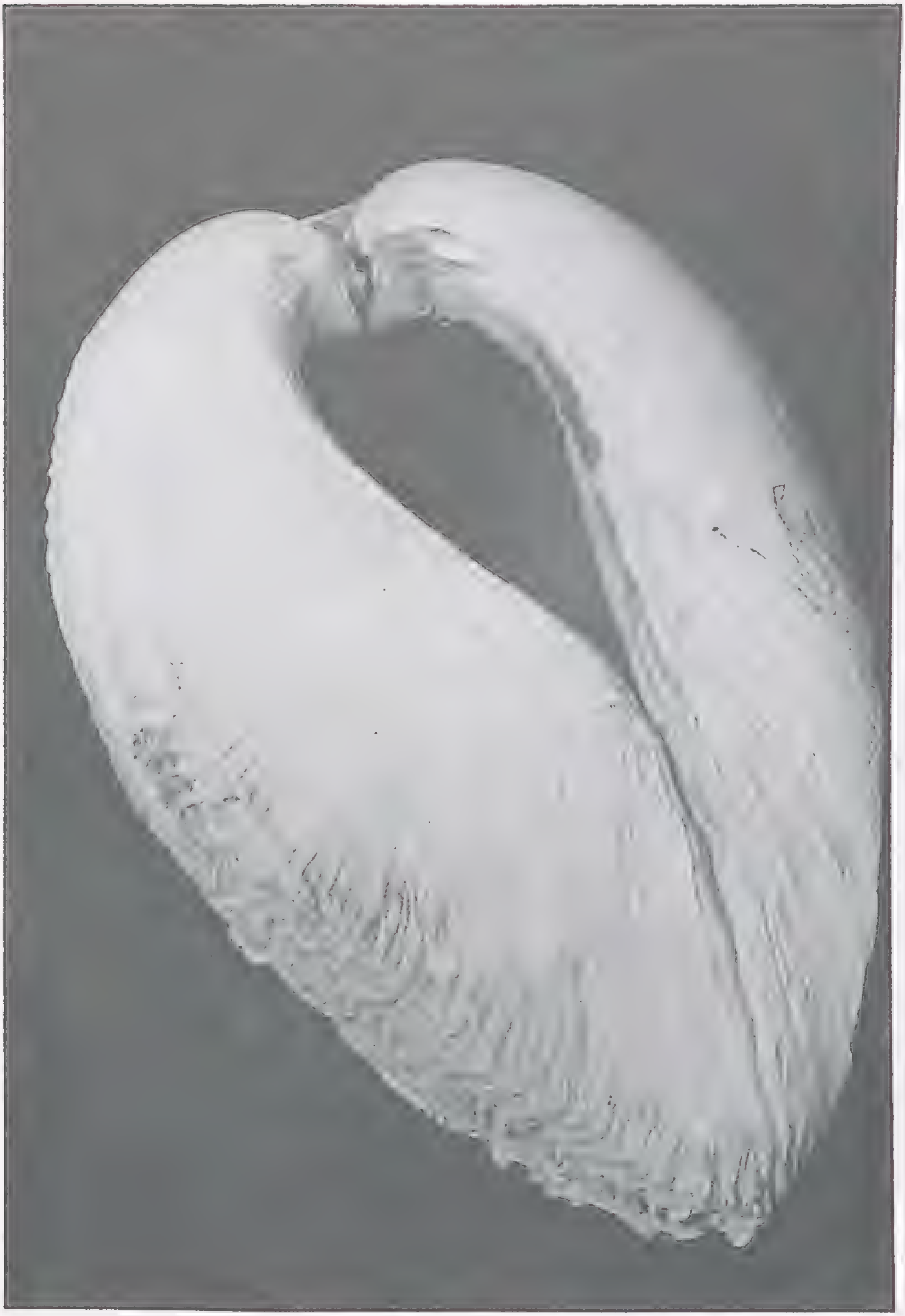

Figure 17. *T. crocea*, under view of shell valves showing large byssal gape with extremely smooth surrounding area probably due to chemical activity, in more peripheral areas scales worn down by mechanical action; no byssal funnel.

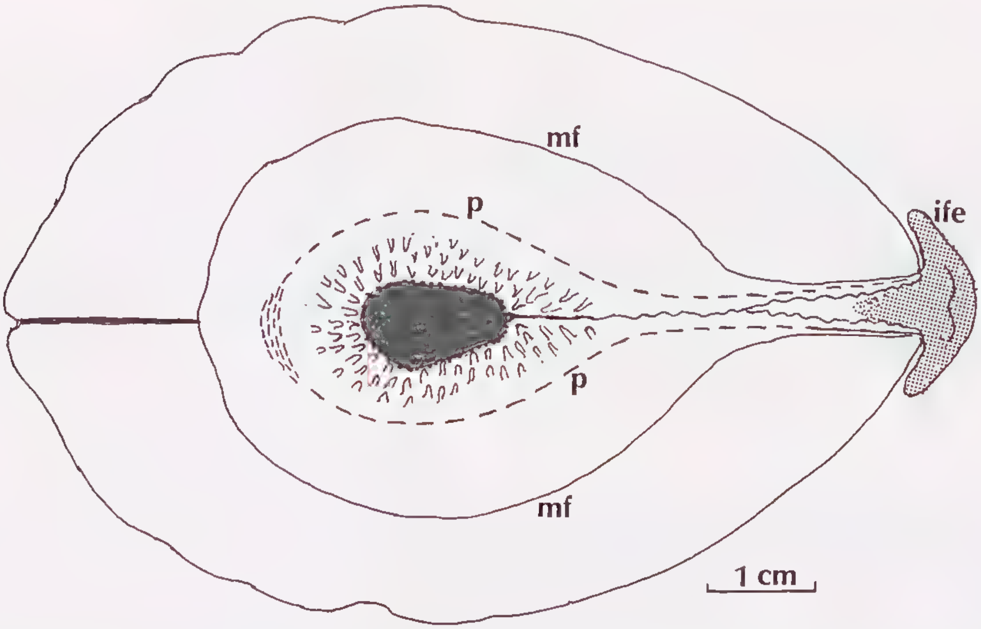

Figure 18. *T. crocea,* under view showing more condensed byssal mass (cf Fig. 10) with wide extension of peripheral regions of the middle mantle fold (mf) reaching far beyond the region of periostracal attachment (broken line).

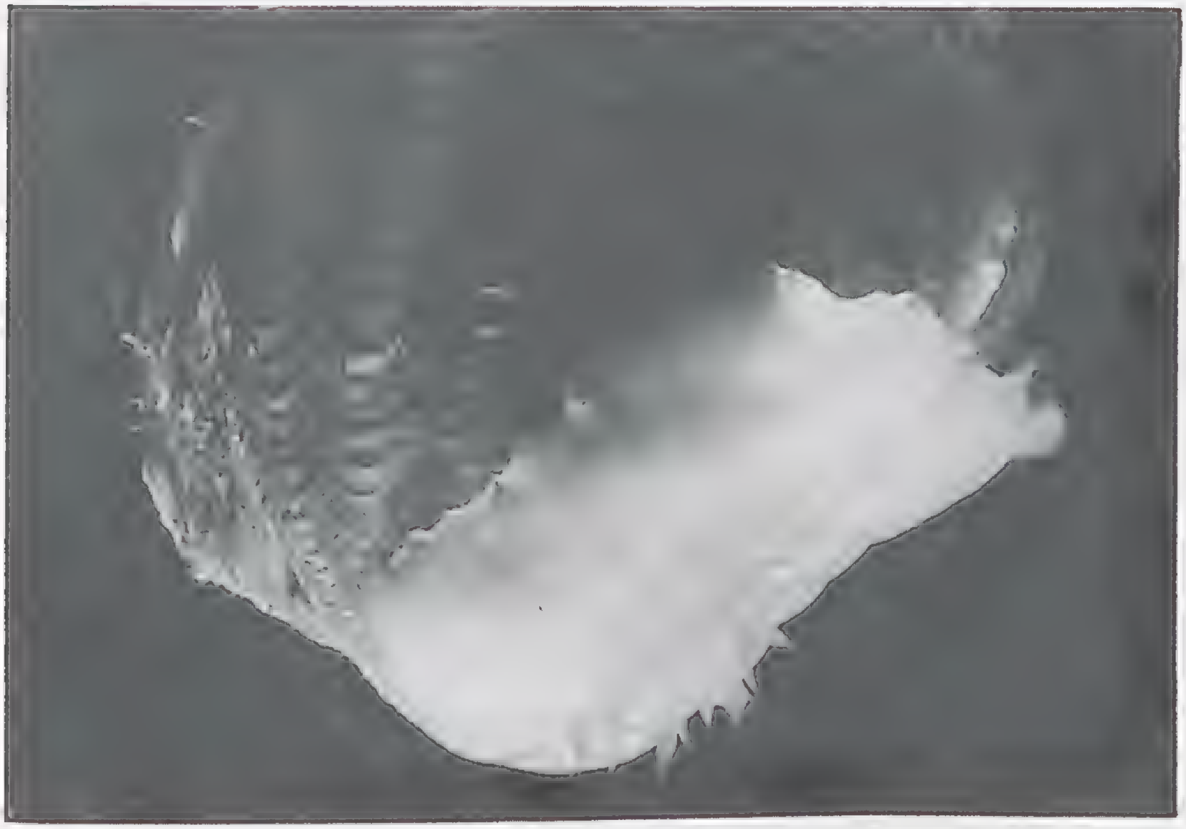

Figure 19. *T. crocea,* under view of living animal showing extended middle mantle folds (white on dark shell) with tentacles on proximal area, i.e. *in situ* around byssal mass. (Photo Martin Jones).

The shell is somewhat longer and also wider than the opening into the boring which has to be enlarged before the animal can be withdrawn. The byssal gape (Fig. 17) is relatively both longer and broader than in other tridacnids allowing egress for a larger and more concentrated accumulation of byssus threads (Fig. 18). There is occasionally some adventitious shell secretion but only at the extreme umbonal end (Fig. 17) and below the level of the gape; there is here no danger from intruding predators. The boring conforms in shape with that of the shell, a ridge along its under surface corresponding to the depression between the valves in the umbonal region. This ridge may culminate, below the gape, in a pillar to which the byssus is attached. This identity of shape between shell and boring is true of all cases where the bivalve does *not* rotate as it bores (e.g. *Platyodon* and *Botula;* Yonge, 1951, 1955).

Scales are formed on the valves only to be worn flush with its surface except near the upper margins. There is no trace of them in the umbonal regions where the surface is completely smooth (Fig. 17). Boring was earlier regarded (Yonge, 1936) as entirely mechanical but this now appears to be untrue. When borings are opened along one side, so as to expose the under surface of the animal without disturbing attachment, considerable extrusion of the middle mantle folds from the byssal gape is often observed and this may also occur after removal from the boring as shown in Fig. 19. The proximal regions of these middle folds carry tentacles as in the other species but the here more extensive distal regions are smooth. Because extended far beyond the line of periostracal attachment, these folds have inner and outer surfaces applied respectively to the umbonal surface of the valves and to the surface of the boring in that region. This great extension of the middle mantle folds supplies the explanation for the description (with a somewhat imaginary figure) of a "mushroom-shaped foot" by Hedley (1921).

These extensive tissues applied to the extremely smooth (umbonal) area of the shell obviously present the possibility of chemical activity affecting both the shell and the wall of the boring. The original protective covering of periostracum will soon have been removed by abrasion of the shell. Indeed conditions resemble those in *Lithophaga,* all species of which bore almost invariably into calcareous rocks and many of which are extremely common on coral reefs. These also are byssally attached with middle marginal fold tissues extending beyond the valve margins at the anterior, here the boring, end (Yonge, 1955). There is evidence of softening of the rock which would assist the undoubted mechanical action of the valves. No secretion of acid has been detected by any worker but that of a chelating mucus from abundant glands in the middle fold has been suggested, most recently by Jaccarini, Bannister & Micallef (1968).

Similar action in *T. crocea* would explain the complete smoothness in the umbonal region. There must, however, be alternate periods of mechanical and chemical activity. During the former the adductors will be relaxed and the opened valves ground against the wall of the boring by the probably alternate contractions of the left and right retractors which are shown, attached to valves and byssus, in Fig. 20. During such mechanical activity no tissues could be extruded through the pedal gape; this would occur when the adductor contracted leaving space between shell and boring. Chemical activity could then proceed over the limited area of initial (i.e. deepest) penetration (precisely as in *Lithophaga).* Such alternation of chemical and mechanical action has been extensively demonstrated in gastropods such as *Urosalpinx* which bore through the calcareous shell of their prey (Carriker, 1969). That bivalves can bore into calcareous rock exclusively by chemical means is shown in *Fungiacava eilatensis,* a mytilid which penetrates through the skeleton of living fungid corals exclusively by means of a "pallial envelope" composed of the middle marginal folds which *completely enclose* the excessively delicate valves (Goreau, Goreau, Soot-Ryen & Yonge, 1969). This undoubted chemical boring is probably the best evidence that similar, probably chelating, activity occurs in *Lithophaga* and *T. crocea*.

In the original description of boring (Yonge, 1936), it was suggested that this took place diagonally, the pillar to which the byssus is attached needing to be continuously undercut. Later Purchon (1955) considered that the attachment area did not change position, byssal threads being worn away during growth and replaced by others. However the problem is changed if the pillar is subject to continuous chelating action; indeed examination of a large series of borings shows wide variation in the size of the pillar in some cases reduced to an irregular spine in the middle of the byssal threads. It is now thought that *T. crocea* bores straight down, the pillar largely eroded by chemical means and new byssal threads attached.

(c) "Giant" Species *(T. gigas, T. derasa).*

Starting with the structure and mode of life in *T. maxima* and *T. squamosa,* further adaptations within the genus lead either to the appearance of the smaller boring *T. crocea* or else to that of much larger species which lose attachment. Judging by the partial closure of the byssal gape already mentioned in the large specimen of *T. maxima,* such increase in size is possibly *inevitably* accompanied by reduction and closure of the gape with atrophy of the byssal apparatus and retractors and reduction of the marginal folds on the under side. It is uncertain precisely at what size these giant species lose attachment but Rosewater (1965) in his plates 278 and 281 shows shells of *T. gigas* and *T. derasa* respectively 123 and 258 mm long both with an apparently functional byssal gape. Owing to the breadth of the under surface in these enlarging animals a stage must come when no predator can make its way into the now increasingly reduced byssal gape. Certainly the mantle margins on the under side will cease to have any but the primitive function of shell secretion. This, however, is now most actively taking place throughout the general surface of the mantle which secretes what eventually must become enormous thicknesses of the porcellaneous inner calcareous layer (Taylor, Kennedy & Hall, 1969). It is the thickness and so weight of the under (umbonal) areas of the valves which maintains the adult posture in these species.

Specimens of *T. gigas* 740 mm long and of *T. derasa* 380 mm long were examined at Lizard Island in 1975. The byssal apparatus was lost in both but a reduced, flaccid foot persisted in the former without trace of retractors although relatively slender muscles persisted in the other. Stasek (1962) revealed interesting differences in the ctenidia, those of *T. gigas* do not significantly differ from those in other species of *Tridacna* but in *T. derasa* unique "plical nodes" occur in rows parallel to the free margin across the face of the lamellae. The ctenidia also extend anterior to the labial palps with which they are connected by way of long distal oral grooves. The significance of these features remains to be determined.

The exceptional size attained by these two tridacnids may reasonably be attributed to their capacity for "farming" algae in the still larger siphons (Fig. 21). This additional source of food, the quantity of which *automatically increases as the animals increase in size,* removes the limitations in size which are imposed by even the most efficient ciliary feeding mechanism. Speed of calcification is also involved. By the aid of radioautography, Bonham (1965) suggests that one specimen of *T. gigas* increased in shell thickness by 10 mm annually. This is sixteen times the increase noted by Wilbur and Jodrey (1952) in the oyster *Crassostrea virginica* which is a rapidly growing bivalve. Observations on a second specimen of *T. gigas* indicated even greater speed of calcification, the animal reaching a length of 550 mm in an estimated period of six years. Although there is very little evidence about growth rates in other bivalves, Bonham

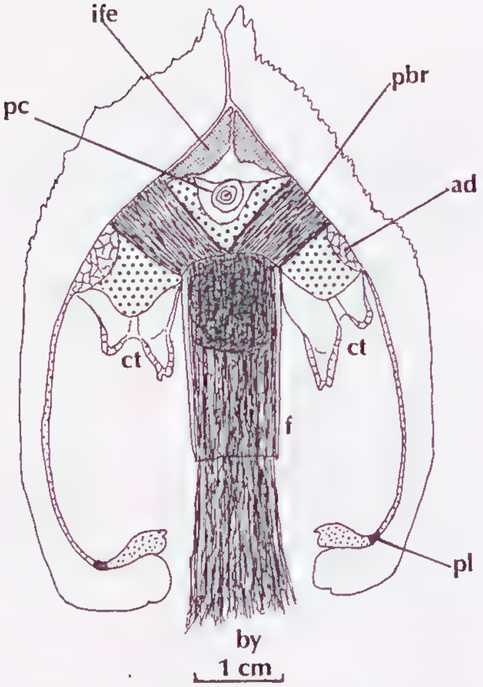

Figure 20. *T. crocea*, preserved specimen frozen and cut transversely, showing mode of byssal attachment with posterior byssal retractors attached to upper region of shell valves, probably contracting alternately when boring, outer surface of under regions of valves worn smooth by boring.

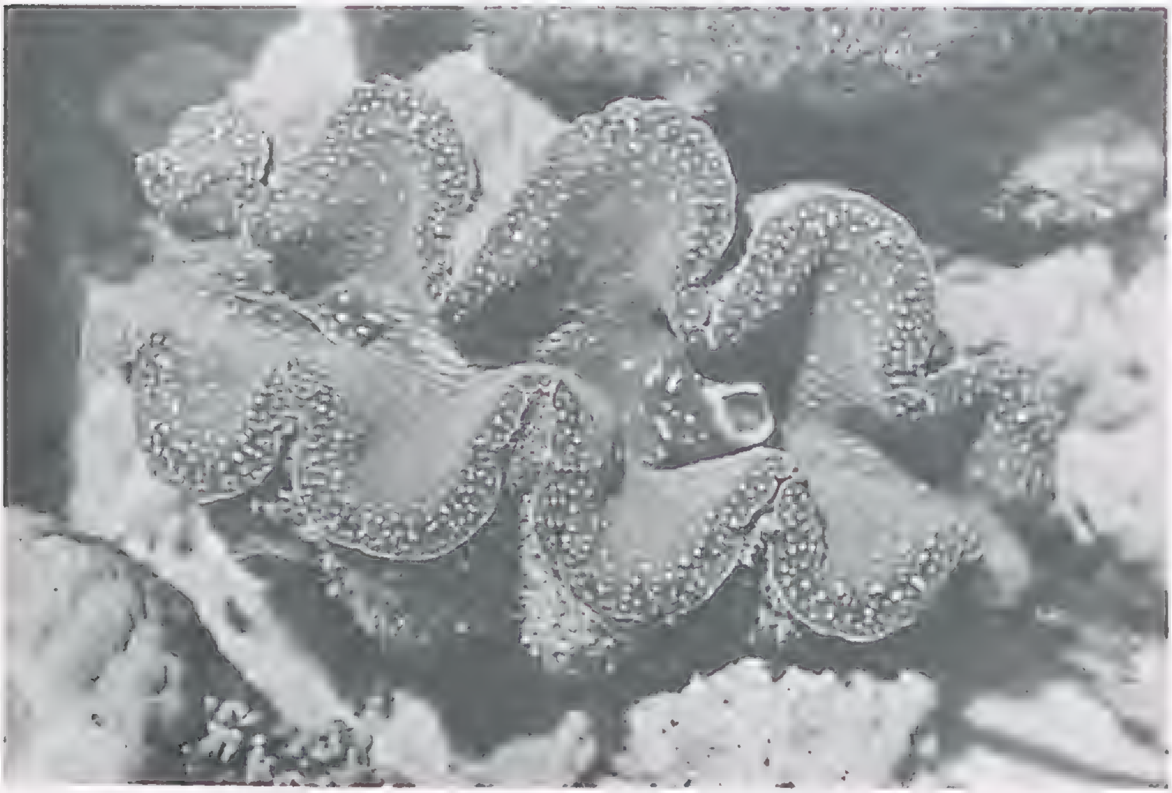

Figure 21. *T. gigas*, fully expanded under minimum depth of water, Low Isles, N. Queensland. (Photo M. J. Yonge).

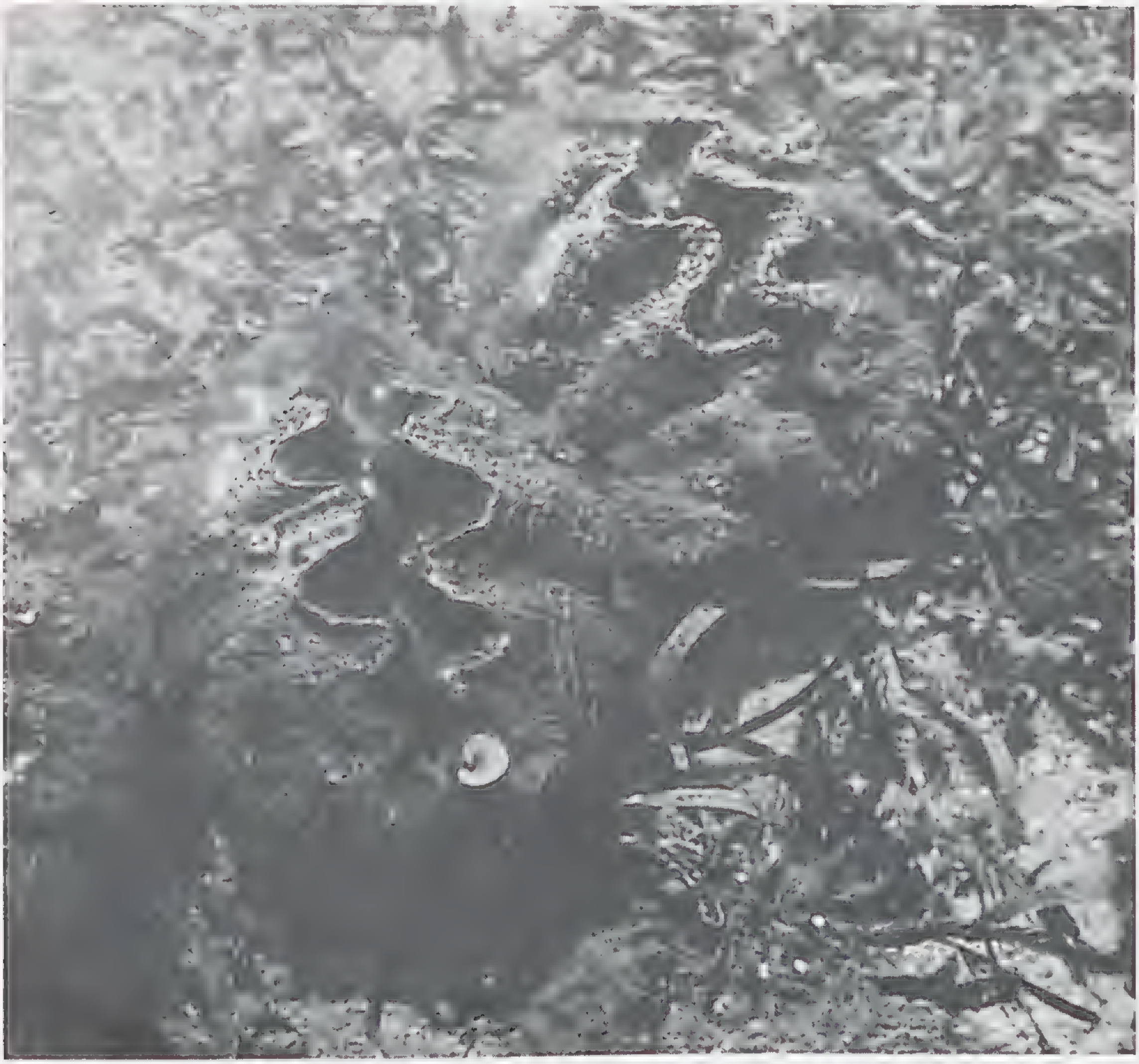

Figure 22. *Hippopus hippopus*, two specimens on sandy area with turtle grass, *Thalassia hemprichii*, on lee of reef flat, Low Isles. (Photo M. J. Yonge).

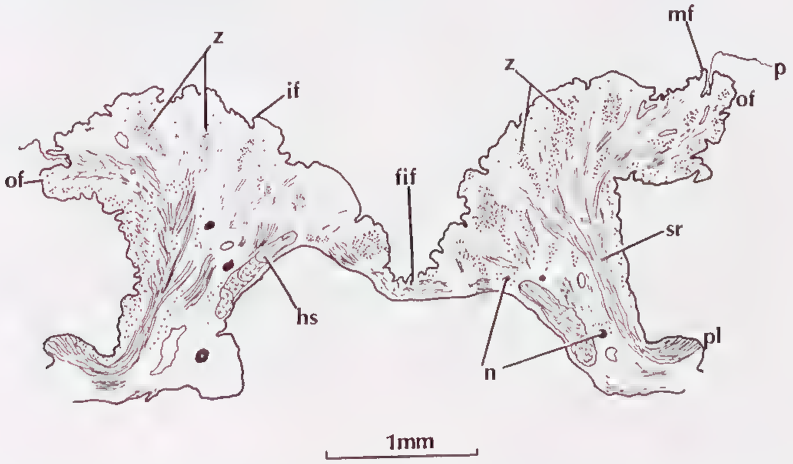

Figure 23. *H. hippopus*, transverse section through middle of upper surface, between siphonal openings, inner folds hypertrophied but without the extensions present in *Tridacna*.

concludes that tridacnids are the fastest growing of all bivalves. In support, however, may be quoted the estimates of McMichael (1974) that *T. maxima* attains lengths of around 160 mm in eight years although then slowing down to reach an eventual length of some 240 mm after 40 years. In hermatypic corals the zooxanthellae are essential in the necessarily high rate of calcification (if reefs are to be maintained in shallow seas). This may prove to be true also of the Tridacnidae.

Adaptation in these giant species consists essentially of still greater increase in size (*all* Tridacnidae are exceptionally large bivalves). On the upper surface of the animals this results in still further enlarged siphons (Fig. 21) with a greater capacity for housing zooxanthellae and so the increase in nutrition this must represent. On the under side it involves a simplification, the loss of the byssal apparatus and the byssal gape, with only the outer marginal folds of the mantle retaining any function. Greater increase in shell thickness (calcification possibly enhanced by greater algal populations) ensures continued and secure stability with the animal resting on the broad umbonal surface of the enormously thickened shell valves.

(d) Horse-hoof Clam *(Hippopus hippopus)*

Although basic morphology is similar, *Hippopus* differs from *Tridacna* significantly and in ways largely associated with its different mode of life. The siphons are similarly hypertrophied but the inner mantle folds do not extend beyond the margin of the valves (Fig. 22). These invariably separate widely to reveal, stretching between them, a flat expanse of invariably translucent olive green tissue with a superficial pattern of fine, more or less parallel, wavy lines. The elongate inhalant aperture, about a quarter the length of the shell, is usually widely open and edged with a few fine tentacles valueless as strainers. The very mobile exhalant aperture is shorter and points more anteriorly than in *Tridacna*. There is the same immediate reaction to the shadows and other stimuli although there are *no eyes* or other obvious receptors.

In transverse section (Fig. 23) the massive inner folds without extensions are penetrated by numerous strands of muscle and by many blood sinuses. Zooxanthellae are less numerous than in *Tridacna* spp., and both middle and outer folds are still smaller, especially the former which is also pigmented. Unlike *Tridacna,* the periostracal groove occupies the usual position at the base of the somewhat deeper outer fold which is pigmented with iridescent spots. On the under side pigmentation continues along the region of fusion posterior to the byssal gape (Fig. 24). Around this all mantle folds are small, the middle ones bearing only a row of small tentacles, the outer ones, as described below, growing anteriorly *within* (topographically *above)* the (umbonal) region instead of outward and so around this as in the byssally attached species of *Tridacna*.

The general structure of an unattached animal 100 mm long is shown in Fig. 24. Compared with *Tridacna* spp., the adductor is more central while the foot and retractors are reduced. In an attached animal 62 mm long these muscles were 30 mm long by 25 mm broad but here they are reduced to small remnants attached to the anterior sides of the adductors under the kidneys and *not* to the valves. The small anterior retractors (apr) persist. Survey of all available specimens revealed that the byssus has usually been lost in animals 80 mm long although traces persisted in one 120 mm in length. In the largest animal 370 mm long, 300 mm broad and 280 mm high, every trace of the retractors had gone. Other organs in the mantle cavity have the form described by Stasek (1962) although in no specimen personally examined did the outer demibranchs possess the food groove he figures.

The shell, described by Rosewater as having "an elongate triangular outline", demands careful description. Starting with an elongate "tridacnid" form, with growth it

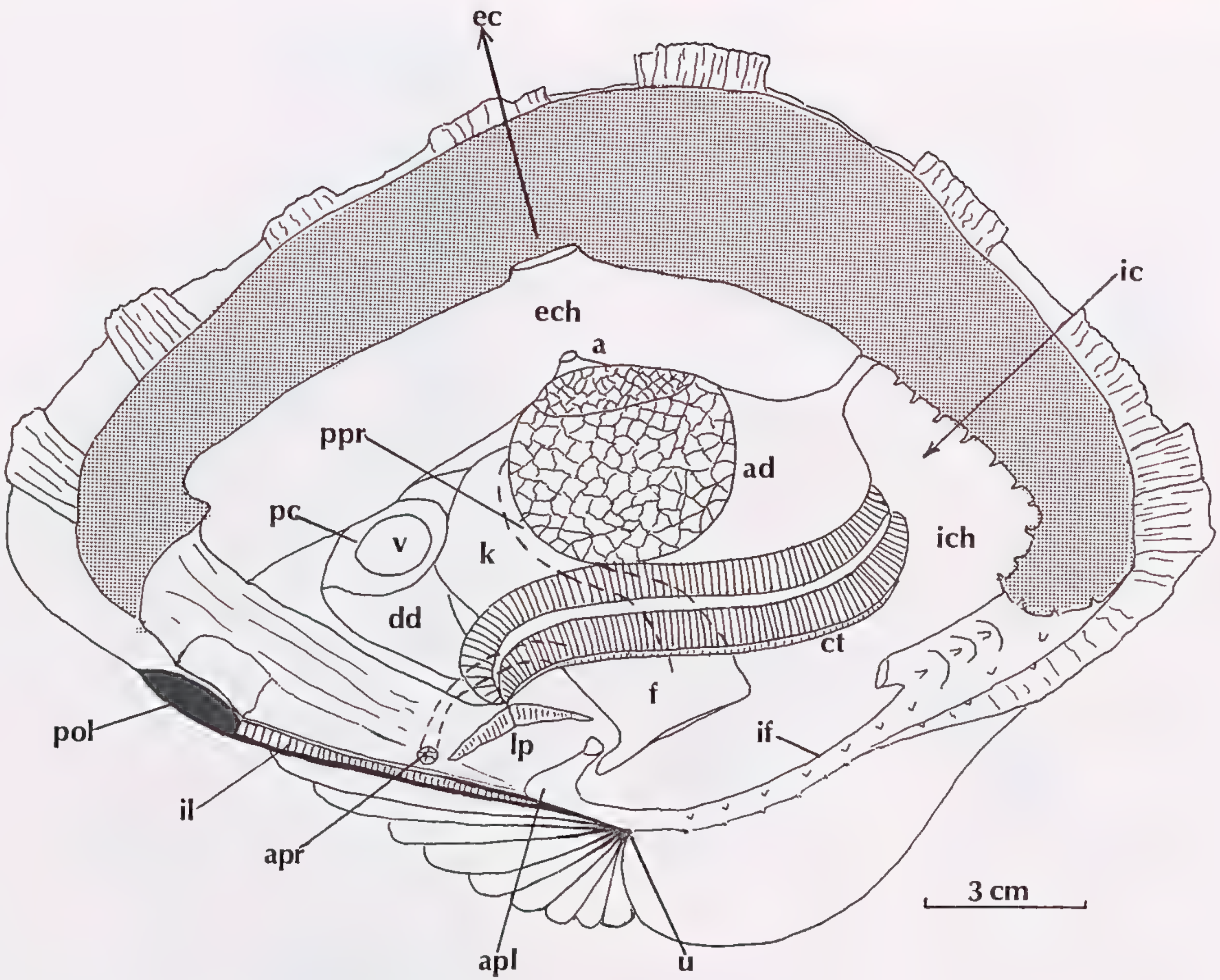

Figure 24. *H. hippopus*, unattached animal viewed from left after removal of valve and mantle lobe. Note details of pedal muscles and anterior extension of pallial tissues (apl) within umbonal region.

becomes broader and higher in relation to length so that large, i.e. unattached, individuals become increasingly globular. On the upper surface the obvious feature is the exact interdigitation of sinuous valve margins. What matters is the precise fit achieved when the adductor contracts. As indicated in Fig. 24, the under surface is sharply differentiated into a posterior region (in relation to the viscero-pedal mass) which is flattened in younger attached individuals (when it includes the byssal gape) but later becomes increasingly concave, the older, unattached animals resting either on this surface or on the more convex but broad anterior (umbonal) region.

This change in form is the consequence of two growth processes. The first, due to the growth gradients around the generative curve along the upper surfaces of the valves, produces the very marked increases in convexity shown in the sections through valves of different sizes in Fig. 25, a-d and e-g. At the same time the valves thicken greatly by additions to the inner porcellaneous layer. As in the giant clams, this is a major factor in stability. As appears in Table 1(a), this growth change has the added effect of increasing height in relation to length and so further contributing to the alterations leading to a more globular form.

The other growth change is on the under surface and involves a relative reduction in length. As shown in Fig. 24, the mantle margins (apl) bounding the umbonal end of the "pedal gape" (which persists as a region of *pallial* separation after byssus and foot are respectively lost and reduced) extend anterior to the umbones (u) morphologically beneath (but topographically above) the posterior end of the hinge region. This also causes an increasing separation of the umbones as displayed to maximum extent in the large shell shown in Fig. 26. These differences from conditions in *Tridacna* appear to be due to the local appearance of a tangential component in shell growth which is exhibited to its fullest extent in the Chamacea and Hippuritacea (Yonge, 1967) and in *Cleidothaerus* (Morton, 1974; Yonge & Morton, 1980). In these bivalves the effect of this component dorsally is to split the hinge anteriorly with wide separation of the umbones, and to extend it posteriorly. In *Hippopus* its effects are confined to the anterior (umbonal) end with consequent production of the beginning of a spiral in each valve, new shell being secreted between the increasingly separated umbones (Fig. 26). The overall result is to cause a rotation of the mantle/shell but in a *clockwise* direction and so in opposition to the other movements of the pallial tissues in relation to the viscero-pedal mass. Measurements given in Table 1(b) reveal the increasing extent to which, with growth, the anterior pallial boundary (Fig. 24, apl) advances beyond the line of the umbones, namely from 2.3% of total shell length to 19% with increase in shell length from 43 to 395 mm This represents a significant "telescoping" and a reduction in shell length in relation to other shell dimensions.

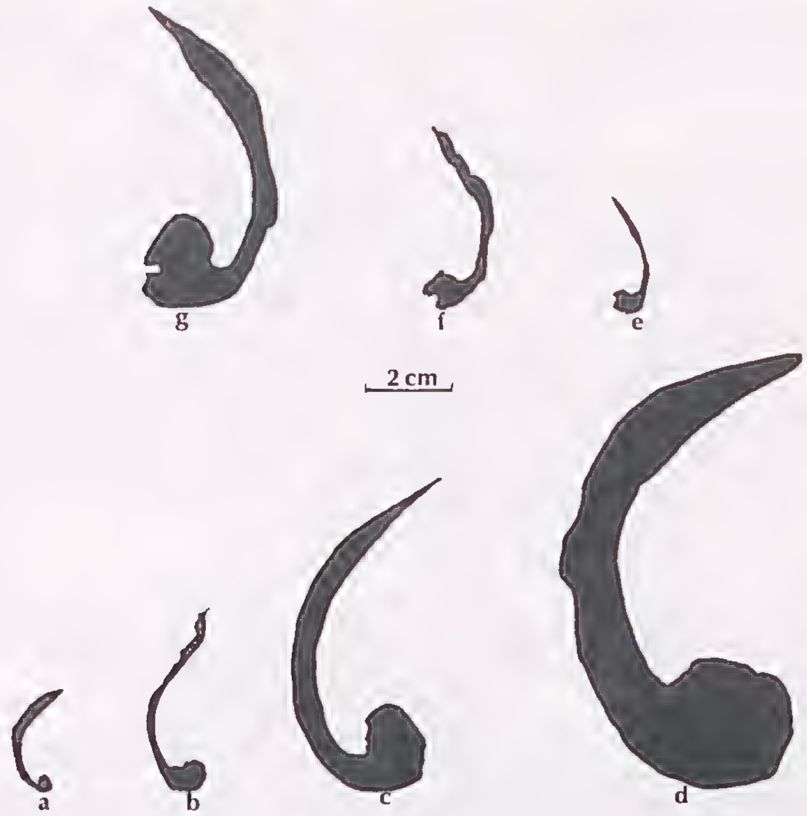

Figure 25. *H. hippopus*, sections through resin embedded valves of various sizes showing increase in thickness, especially basally, with age, and accompanying loss of byssal attachment.

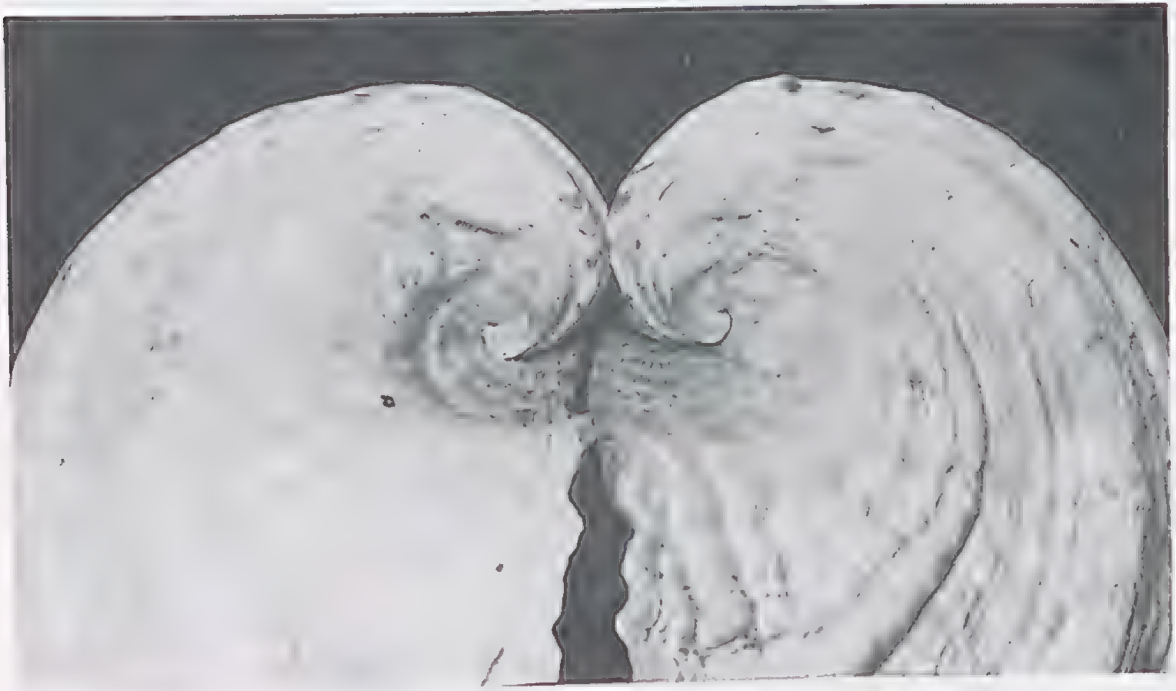

Figure 26. *H. hippopus*, under surface of large shell (395 mm long) showing wide separation of umbones due to effect of tangential component in shell growth. (Photo A.I.M.S.)

TABLE 1. *H. hippopus;* changes in the relations of different regions during growth. (a) Relation of height of shell to length; (b) Relation of anterior end of mantle lobes ("pedal gape") to line of separated umbones.

| **(a) Length in mm** | **Height in mm** | **Ratio H/L** | **(b) Extension of mantle lobes anterior to umbones in mm (Fig. 24, apl-u)** | **Relation of this to shell length** |
|---|---|---|---|---|
| 43 | 28 | 65% | 1 | 2.3% |
| 63 | 44 | 70% | 2.5 | 4.0% |
| 90 | 74 | 82% | 6 | 6.7% |
| 98 | 71 | 73% | 6 | 6.1% |
| 115 | 81 | 70% | 8.5 | 7.4% |
| 130 | 104 | 80% | 15 | 11.5% |
| 135 | 100 | 76% | 16 | 12.0% |
| 145 | 111 | 77% | 17 | 12.0% |
| 204 | * | — | 31 | 15.2% |
| 395 | 304 | 77% | 75 | 19.0% |

* irregular

The end result of both growth processes is conversion of an elongate, moderately high although basally always broad, bivalve into one that becomes increasingly globular although with flattened anterior and posterior under surfaces on either of which it can securely rest. Aided by the intimate interlocking of the undulating valve margins, the upper surface is rounded. Projections (not scales) on the outer surface of the valve in small attached individuals are not present on the larger valves of older animals which thus offer no resistance to being turned over and then back. All of these characters, with absence of any overlapping of the valve margins by the siphonal tissues so that valves can close quickly, enable *Hippopus* to be rolled about with impunity.

Available evidence suggests that settlement takes place on seaward surfaces. Later, when attachment is lost young animals will be carried over the surface of the reef where individuals will find temporary or permanent rest in suitable depressions. But the ultimate site of most of the larger animals is on sandy areas in the lee where they may be the most conspicuous member of the fauna as with those shown in Fig. 22 living on sand among growths of turtle grass, *Thalassia hemprichii*. Large numbers of *Hippopus* were viewed on sandy areas to the west of the anchorage at Low Isles during 1928/29 and, despite great deterioration in the fauna generally due to sedimentation, they appeared just as numerous when the same sandy areas were revisited during February 1978, scores of large animals being seen. The only attached animal noted during this brief visit, and actually the smallest one recorded in Table 1, was collected on the exposed southeastern surface of the reef.

Although in constant danger of being rolled over in the surf generated by the trade winds, *Hippopus* is always found upright after it loses attachment. This is due to the great thickness of the umbonal regions of the shell which steadily increases after detachment as shown in Fig. 25. The final enormous thickness in a shell 340 mm long is illustrated in Fankboner (1971a, Fig. 1). This great basal weight represents a self-righting mechanism as noted by Purchon (1977) and by Fankboner. But whereas the former considers that the animals immediately right themselves when rolled over, Fankboner regards righting as a step-wise process. The animals remain on their sides until the adductors relax when the upper umbone will no longer lie directly above the under one. The unbalanced shell then rolls over with both umbones coming to lie undermost when balance is regained. Personal observations support Fankboner's conclusions.

*Hippopus* is, therefore, unique among bivalves because adapted, after initial attachment in exposed areas, for being rolled to leeward by prevailing seas, never re-attaching itself as McMichael (1974) has shown may happen with *T. maxima*, but maintaining an essential upright posture. It thus becomes the only tridacnid able to exploit life on the sandy leeward extensions of reefs. It shares this capacity with the similarly specialized hermatypic Fungiidae (also with the Atlantic *Manicina (Maeandra) areolata)*. These corals also start life attached, being later carried to leeward, often on to sandy areas. They are there capable of uncovering themselves when buried under sand during storms (Marshall & Orr, 1931; Yonge, 1935) and also of righting themselves when turned over (Abe, 1939). *Hippopus* is too large to be buried but is beautifully fitted for righting itself when rolled on to one or other side.

## ZOOXANTHELLAE

The supreme significance of the zooxanthellae[1] is here taken for granted with the unique tridacnid form the direct consequence of structural changes ensuring their more extensive housing and maximum exposure to light. Further research is for others to whom the electron microscope and facilities for physiological and biochemical investigation are available. Nevertheless some assessment of the present state of knowledge about the interaction of symbiont and host appears necessary, the more comprehensive owing to the recent general review by Dr R. K. Trench (1979) and information kindly supplied by him about the conclusions contained in a joint paper dealing specifically with symbiosis in the Tridacnidae and still in the press (Trench, Wethey & Porter, 1981).

Early personal conclusions about the nature of the association (Yonge, 1936, 1953a) were that the algae present and often observed dividing in superficial tissues were always contained within blood cells. These were regarded as being later responsible for conveyance of senescent algae into the visceral mass where they were digested within these phagocytic amoebocytes. Removal of the waste products of digestive processes carried out in the blood stream was held to explain the uniquely large size of the tridacnid kidney (Fig. 27). No passage of zooxanthellae into the gut was noted, those found there were assumed to have entered following rupture of the tissues prior to examination.

Subsequent research has not supported these views. Using the electron microscope, Kawaguti (1966) found that in *T. crocea* the zooxanthellae are usually free although sometimes they are "accompanied by" or "coated with" blood cells. Fankboner (1971b), also using electron microscopy, concluded that "senescent zooxanthellae are selectively culled from the algal population of the mantle edge" (i.e. of the siphons) "by amoebocytes and are intracellularly digested via amoebocyte lysosomes both in the circulatory system and the interdiverticular spaces of the digestive gland."

Morton (1978) who accepts the view that zooxanthellae may be contained within amoebocytes describes, again in *T. crocea*, a diurnal pattern of activity with clusters of

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[1] Nomenclature raises problems. When initially cultured and shown to be dino-flagellates, Freudenthal named these organisms *Symbiodinium microadriaticum* the generic placing later changed by Taylor to *Gymnodinium*. With discovery that thecal plates occur in motile stages, Loeblich and Sherley (1979) now place *Symbiodinium* Freudental in the synonymy of *Zooxanthella* Brandt. Trench (1979) retains the generic name *Symbiodinium* and is here followed.

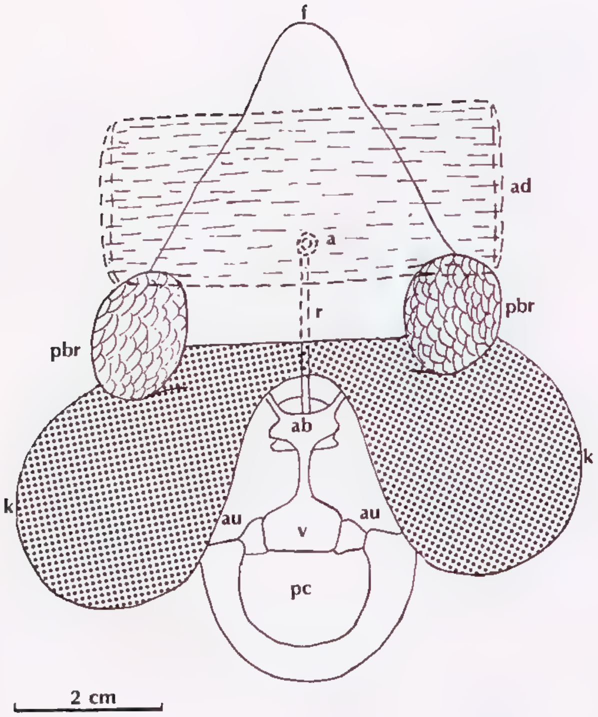

Figure 27. *T. squamosa*, visceral mass viewed from antero-dorsal aspect showing pericardium with contained heart with aortic bulb and hypertrophied kidneys characteristic of the Tridacnidae.

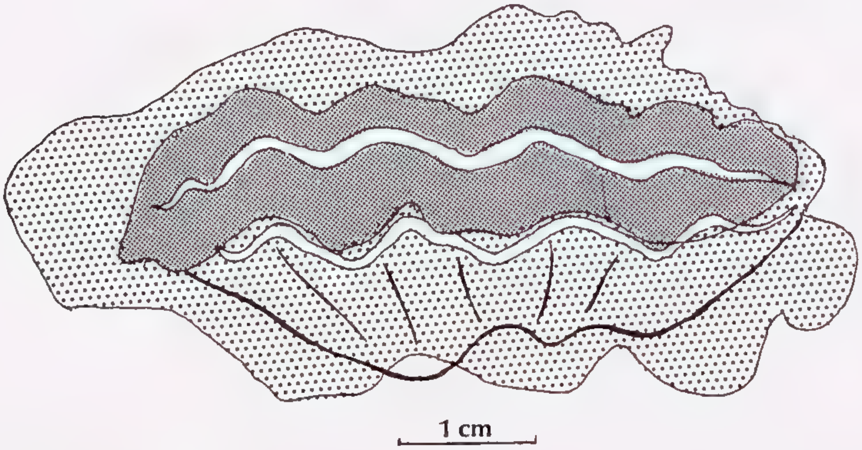

Figure 28. *T. crocea*, result of time/lapse photography over day and night. Coarse stippling indicates full extent of siphonal expansion, as at 1345 hrs. but maintained during daylight; fine stippling, extent of expansion during night, actually as at 0100 hrs. but maintained continuously presumably by partial contraction of siphonal retractors. Sinuous white areas indicate margin of valves exposed during rare contraction of adductor.

zooxanthellae and amoebocytes appearing within the digestive cells of the digestive diverticula around dawn. These appear in great numbers in the lumen some two hours later after the distal two thirds of the digestive cells disintegrate. This he relates to a diurnal pattern of feeding and digestive activity he has described in other bivalves. He also reports some passage of zooxanthellae into the kidneys.

Without attempting to confirm his general results the opportunity was taken of the presence of skilled photographic assistance at the Australian Institute of Marine Science in 1978 to carry out a series of time/lapse photographs of *T. crocea* over periods of around 48 hours. The results are indicated in Fig. 28. Morton had recorded the extent of adduction kymographically and found that during the night the valves gaped slightly with few adductor contractions whereas during the day they gaped widely with frequent adduction. Photographic data only revealed the degree of expansion of the siphons which was at least 50% greater during the period of light than during the night. Sudden withdrawals for which the siphonal retractors must have been solely responsible occurred at all times and would be great enough to expel water from both inhalant and exhalant openings to remove pseudofaeces and faecal pellets respectively. Greater withdrawals involving contractions of the adductor which may be frequent in nature where predators abound were rare in the undisturbed laboratory conditions. They were revealed by the occasional appearance on the film of opposing sinuous white areas (Fig. 28) due to complete withdrawal of the siphons and exposure of the margins of the white shell valves. The consequent back pressure of blood within the siphons would explain the large aortic bulb (Fig. 27, ab) present in all tridacnids. In other bivalves this is associated with the variable pressure of blood within the actively burrowing foot.

Using the electron microscope, Trench, Wethey and Porter (1979) find no evidence that either in superficial or in the deeper regions, i.e. within the visceral mass or in the lumina of any region of the gut, are the algae contained within blood cells. They find that degenerate zooxanthellae occur even in the siphonal regions while intact, and demonstrably living, zooxanthellae are voided with the faeces. Unlike Morton, they find no trace of zooxanthellae within the kidneys, not even indications of algal pigments. But the tridacnid kidney is enormous. For instance in a specimen of *T. derasa* examined at Lizard Island, the total wet weight of the tissues was 1070 grams, with siphons 280, adductor 260, visceral mass 389, foot 40, and kidneys 101 grams. It is difficult not to associate this enormous organ, 1/10th of the total tissue weight with the presence of symbiotic algae.

There is also the problem of the regulation of the numbers of contained symbionts which are continually increasing by division in superficial areas. This affects all cases of plant/animal symbiosis and has recently been reviewed by Muscatine and Pool (1979). In the Tridacnidae control appears to be exercised by the periodic outward passage of excess numbers of algae via the digestive diverticula into the lumen of the gut as demonstrated by Morton. This is essentially similar to what occurs in hermatypic corals where any excess is removed by way of the absorptive/excretory zone of the mesenteries and is dramatically increased when corals are stressed by exposure to sublethal temperatures or very low oxygen tensions (Yonge & Nicholls, 1931) or to greatly lowered salinities (Goreau, 1964).

Earlier views that tridacnids acquire energy from the algae by digesting them appear at best only partially true. Exposure of specimens of *T. maxima* to water containing $^{14}C$ (Goreau, Goreau & Yonge, 1973) resulted in the appearance within ten minutes of radioactivity within zooxanthellae in superficial regions and later in more deeply situated algae. This radioactivity passes out of the zooxanthellae as a result of the nutrient movement from symbiont to host of the photosynthate (Muscatine, 1967; Smith, 1979). It was then identified in all the major centres of metabolic activity, namely in the byssal gland, periostracal groove, pallial and ctenidial mucous glands and, most strikingly, in the cells of the minor typhlosole of the style sac providing evidence that the style can be completely replaced in 73 hours. It was concluded that the Tridacnidae obtained the major benefit from their symbionts by way of these released photosynthates predominantly composed of glycerol and alanine (Smith, 1979; Trench, 1979). While it is impossible at present completely to dismiss the possibility that some energy is obtained by digestion of senescent algae within phagocytic amoebocytes (intact ones are now known to pass unchanged through the cells of the digestive diverticula), this does appear to be of minor significance. Indeed Trench (1979) states that "good evidence for digestion of zooxanthellae by animal hosts is lacking."

What has been stated above roughly covers the present state of knowledge and does at least show the need for more extensive and precise information on the role of the hypertrophied kidneys and the relative importance in nutrition of the "imprisoned" phytoplankton of zooxanthellae and the external supplies of "free" phytoplankton collected and utilized by the unmodified organs of feeding and digestion. The great importance of the former, already stressed as responsible for the large size of the Tridacnidae culminating in the unique dimensions of the giant species, is strikingly indicated by the earlier mentioned observations of Salvat (1969, 1971) in the Tuamotus. The enormous populations of *T. maxima* found in the closed atolls where no phytoplankton from surrounding waters is available is the best present evidence of the overwhelming importance as food to the animal of the contained zooxanthellae. Recently Ricard and Salvat (1977) have shown that *T. maxima* lives as well without as with available phytoplankton; also, from discharged zooxanthellae, much protein is added to the lagoon water.

## EVOLUTION

While basic structure, both of mantle/shell and viscero-pedal mass, indicates association with the Cardiidae and Hemidonacidae in the superfamily Cardiacea, the totally distinctive structure of the Tridacnidae indicates long and intimate association with coral reefs. As Rosewater (1965) notes, they "are obligatory inhabitants of the shallower waters of coral reefs." Taking information from the *Treatise on Invertebrate Palaeontology*, the Cardiacea appeared in the Upper Triassic with the earliest tridacnids not until the early Tertiary, possibly the Upper Cretaceous.

The Cardiacea appear always to have been superficial burrowers with very short siphons (absent in the Hemidonacidae) acquiring a characteristically large foot, angulate in the Cardiidae and compressed in the Hemidonacidae, enabling them to move through and, in the former often over, the substrate (Ansell, 1967). In this family a byssus may, although rarely, be retained into adult life as in *Corculum*. Members of both of these families live exclusively on soft substrates. *Corculum*, however, comes eventually to final byssally attached settlement on dead coral rock thinly covered with sand (personal observations). The story is different in the Tridacnidae which are basically adapted for life on hard substrates, i.e. become epifaunal instead of infaunal. The byssal apparatus is retained into adult life, its formation the sole concern of the foot which atrophies when the byssus is lost in the giant species and in *Hippopus*. In virtue of its size, the last named becomes epifaunistic on a soft substrate.

Shallow coral reef seas, largely formed by hermatypic scleratinian corals presumably with the associated symbiotic zooxanthellae needed to ensure an adequate rate of calcification, appear in the middle Jurassic. The environment the tridacnids were later to exploit was thus created. Their appearance, however, was delayed until the end of the

Mesozoic or early Caenozoic during a period of major decline and change when, as pointed out by Newell (1971), reefs decline and the previously dominant, even reef-forming, bivalve rudists disappear. It is indeed possible that this disappearance left settling space and unexploited phytoplankton food for these early tridacnids. These must initially have maintained position by retention and enlargement of the byssal apparatus with loss of other pedal functions while maintaining exclusive dependence on their ciliary feeding mechanism for food. Possibly they settled in cracks or depressions which, with continued enlargement of the byssal apparatus, ensured survival in these often turbulent waters.

At some stage zooxanthellae were acquired and became housed in the siphonal regions. i.e. those areas alone exposed to light. It is reasonable to assume that the tridacnids were initially infected by algae already adapted for symbiotic existence within hermatypic corals or some of the other numerous coelenterates that harbour them in coral reef areas. In the Scleractinia and other "closed" systems, zooxanthellae are passed from generation to generation via the egg and so, always within the same host environment, would not tend to diverge. This is less probable in "open" systems as in the tridacnids but also the rhizostome medusae, *Cassiopeia* and *Mastigias* (Trench, 1979) and in the gorgonid *Pseudopterogorgia bipinnata* (Kinzie, 1974). In all of these the aposymbiotic post-larvae are infected from the ambient environment which must contain motile stages of zooxanthellae from many sources. Schoenberg and Trench (1979) have demonstrated the presence of 12 strains of zooxanthellae distinct on the basis of isoenzyme patterns and so presumably genetically distinct. It does, however, remain to be demonstrated to what extent "open" hosts are restricted to colonization by particular strains.

The post-larvae of the medusae and the gorgonid will be infected via the mouth, i.e. being taken into the tissue through the "absorptive" region of the gastric ridges or mesenteries. A similar mode of infection remains to be proved in the Tridacnidae. Conditions are vey different because corals, and effectively all other coelenterates, are highly specialized carnivores never reacting to, or being capable of digesting, vegetable matter (Yonge, 1930a, b) whereas plant cells are the normal food of all bivalves. Trench (1979) recognizes this problem but, because there is a route whereby excess of algae are removed from the gut, postulates a similar course for infection. While algae already specialized for life within animal cells may be able to resist the action of digestive enzymes while passing through the cells of the digestive diverticula this may not be true of the motile stages while there is the possibility of direct infection through the exposed tissues around the inhalant siphon. Some evidence in favour of this is provided by Goetsh and Scheuring (1926) who found some specimens of the freshwater bivalves *Anodonta cygnaea* and *Unio pictorum* that were infected around the siphonal regions, to the extent that light reaches, by species of *Chlorella* which were most unlikely to have survived passage through the gut. However further speculation about the original mode of infection must await precise knowledge about how this occurs in modern post-larvae.

Certainly initial infection must have been followed by major changes in form as the siphons enlarged to house ever increasing numbers of algae which rendered the animals ever more independent of the restricted phytoplankton of impoverished coral reef seas. Personal views, strengthened over the years of research on the Bivalvia, are that mantle/shell and viscero-pedal mass with their different symmetries have some measure of independence. In the evolution of the Tridacnidae, it is postulated that natural selection favoured the continued enlargement over the entire upper surface of the siphons which, without loss of their original function, came to house and expose to the light ever greater populations of zooxanthellae. This anterior movement of pallial tissues

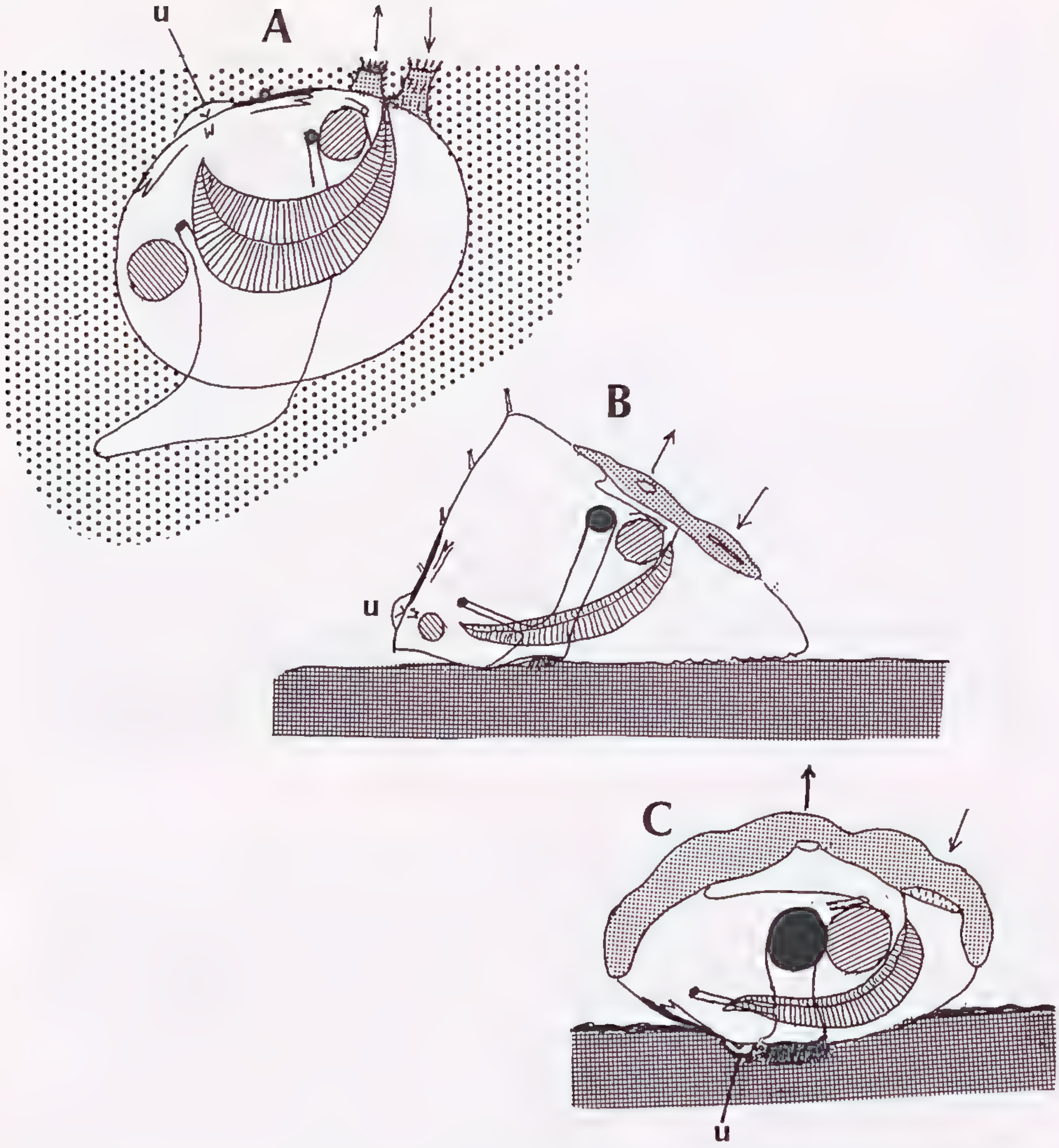

Figure 29. Comparison of basic structure in A, modern cardiid — isomyarian, infaunal; B, Eocene *Lithocardium* — heteromyarian, epifaunal, byssally attached (structure postulated); C. modern tridacnid — monomyarian, epifaunal, byssally attached with some penetration ventrally into hard substrate. Changing position of umbo (u) indicates degree of turning of the mantle/shell in relation to the viscero-pedal mass. Other structures shown:- siphons (stippled), adductors (oblique lines), ligament (black), ctenidia, foot with retractors and (in B, C) byssus, hinge teeth and anus. Arrows indicate inhalant and exhalant currents.

involved that of the shell and only ceased when the anterior end of the ligament came in contact with the byssal mass below. The continued presence of this attachment throughout the entire process held the viscero-pedal mass in position, the foot unalterably ventral. Such views are credible because at no stage do they involve the assumption of structures incompatible with further existence. As noted earlier (Yonge, 1953a), the Eocene *Lithocardium aviculare* (Fig. 29B) with triangular shell, heteromyarian and without anterior lateral teeth and with an assumed byssal attachment is a possible stage in the turning movement of mantle/shell that culminated in the Tridacnidae. This involves extension of the siphonal region with contained zooxanthellae to form an intermediate condition between a cardiid (Fig. 29A) and a tridacnid (Fig. 29C).

Regarding mantle/shell and viscero-pedal mass as an integrated unity, Stasek (1963) has sought to transform the cardiid into the tridacnid form by way of a series of co-ordinates. This, because the two are basically similar, he has succeeded in doing but only as a result of a purely morphological exercise, reminiscent of the "pure morphology" of Geoffrey St. Hilaire. He makes no attempt to follow the structure of the animal during the complex series of changes involved in the "transformation" or to discover whether all stages could have been viable. It seems unnecessary to say more about this, only to repeat what was stated earlier, namely that the course of evolutionary change here postulated is not, and indeed could not, be recapitulated during development.

After the initial appearance of the tridacnid form, *Hippopus* must have separated from *Tridacna* relatively early, presumably before the siphons had begun to extend laterally beyond the margin of the valves. Subsequent evolution, with closure of the byssal gape, must have proceeded independently, the modified shell form in *Hippopus* enabling it to exploit its distinctive habitat on soft substrates.

## ACKNOWLEDGEMENTS

Many acknowledgements are due for assistance in work that has been in progress, off and on, for over 50 years starting with the Great Barrier Reef Expedition 1928/29. The next direct contact with the Tridacnidae came during a period spent as a guest on the Belgian *De Moor* Expedition to the Great Barrier Reef in 1967 and here most cordial thanks are recorded to Professor A. Distèche of the University of Liege, Leader of that Expedition. More intimate contact came in 1975 during participation, thanks to a grant from the Carnegie Trust for the Universities of Scotland, in a malacological "workshop" organized at the Field Station on Lizard Island by Dr Winston Ponder of the Australian Museum. This paper was planned there but it could not have been produced in its final form but for the six weeks in 1978 spent at the Australian Institute of Marine Science at Cape Ferguson, N. Queensland. This was made possible by the invitation of the then Director, Dr Malvin Gilmartin, to participate in the Visiting Scientist Program, work on the Tridacnidae having already been undertaken by Dr W. M. Hamner. At the Institute all manner of assistance was rendered by Martin Jones and Ivan Hauri in whose company Low Isles, the site of the expedition, was re-visited 50 years after the event. The writer has to thank his wife who has assisted so greatly both there and at Edinburgh, also his former research assistant, Jan Campbell (Mrs P. S. Meadows) for certain drawings, Dr R. K. Trench, a one-time co-worker at the Discovery Bay Laboratory, Jamaica and now Associate Professor of Zoology in the University of California, Santa Barbara, for most valuable unpublished information, Professor J. M. Mitchison, F.R.S., for continued use of accommodation and facilities in his Department at Edinburgh and finally the N.E.R.C. for financial assistance provided by Grant GR3/1380.

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Manuscript accepted for publication 21 February, 1980.

ABBREVIATIONS USED IN FIGURES:

| | |
|---|---|
| a | anus |
| ab | aortic bulb |
| abr | anterior byssal retractor |
| ad | adductor |
| aol | anterior outer ligament layer |
| apl | anterior end pallial lobes |
| apr | anterior pedal retractor |
| au | auricle |
| bg | byssal gape |
| bgl | byssal gland |
| by | byssus |
| byf | byssal funnel |
| cp | calcareous plug |
| cs | cardinal socket |
| ct | ctenidia |
| cth | cardinal tooth |
| d | marginal end of depression |
| dd | digestive diverticula |
| ea | exhalant aperture |
| ec | exhalant current |
| ech | exhalant chamber |
| ey | eye |
| f | foot |
| fif | fused inner folds |
| hs | haemal sinus |
| ia | inhalant aperture |
| ic | inhalant current |
| ich | inhalant chamber |
| if | inner fold of mantle margin |
| ife | inner fold extension |
| il | inner ligament layer |
| k | kidney |
| lp | labial palps |
| ls | lateral socket |
| lth | lateral tooth |
| mbg | margin byssal gape |
| mf | middle fold of mantle margin |
| ml | mantle lobe |
| n | nerve |
| of | outer fold of mantle margin |
| p | periostracum |
| pbr | posterior byssal retractor |
| pc | pericardium |
| pg | periostracal groove |
| pga | pedal (byssal) gape |
| pl | pallial line |
| pmg | pallial mucus gland |
| pol | posterior outer ligament layer |
| ppr | posterior pedal retractor |
| r | rectum |
| sc | scales |
| sn 1-3 | siphonal nerves |
| sr | siphonal retractor muscles |
| tm | tentacle on middle fold |
| u | umbo |
| v | ventricle |
| vg | visceral ganglion |
| z | zooxanthellae |

# A REVISION OF THE SPIDER GENUS *BAIAMI* LEHTINEN (ARANEAE, AMAUROBIOIDEA)

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## SUMMARY

The genus *Baiami* Lehtinen is redefined and shown to be typically southern Australian in distribution. Of the nine species considered here, six are described for the first time. New Caledonian elements are excluded from *Baiami*. *Tartarus* Gray is recognized as a junior synonym of *Baiami*. Notes on phylogeny and distribution are given.

## INTRODUCTION

The genus *Baiami* was erected by Lehtinen (1967) for the Western Australian species *Epimecinus volucripes* Simon, 1908 (nominated as the type species of *Baiami*), *E. tegenarioides* Simon, 1908 and *Aphyctoschaema storeniformes* Simon, 1908, and the New Caledonian species *Epimecinus magnus* Berland, 1924 (syn. *E. longipes* Berland — Lehtinen, 1967). Unfortunately, no male material from Western Australia was available so that the male characters of Lehtinen's *Baiami* were based entirely upon those of Berland's New Caledonian species *E. magnus* (Berland, 1924).

Subsequently, Gray (1973) erected the genus *Tartarus* for a male specimen of a highly specialized troglobitic species *T. mullamullangensis* from Mullamullang Cave on the Nullarbor Plain, southern Australia. Since then male specimens of the type species of *Baiami*, *B. volucripes*, have been collected and, together with the type material of *E. magnus* from New Caledonia, examined by the author. This has shown that the New Caledonian species does not belong to *Baiami*; and that *Baiami* and *Tartarus* are congeneric. Consequently, *Tartarus* is synonymized here with *Baiami* and the latter genus is redefined, excluding the New Caledonian material, and is shown to be typically southern Australian in distribution.

*Aphyctoschaema storeniformes* Simon, 1908 is not known to the author. However, its type locality (Daydawn, Western Australia), a surface arid zone habitat, is atypical of the generic distribution as presented here.

## Genus **Baiami** Lehtinen, 1967

*Epimecinus* Simon, 1908: 359-446.

*Baiami* Lehtinen, 1967: 330.

*Tartarus* Gray, 1973: 210. Forster, 1973: 128. New synonymy.

DIAGNOSIS: Retromargin of fang groove with two widely separated teeth; exceptionally with three to five teeth (*B. mullamullangensis*). Median apophysis of palpal organ absent. Conductor a broad, curved membrane with two distal sclerotised processes. Retrolateral tibial process of male palp a basal lamina surmounted by a curved spiniform process. Epigynum with a median fossa, without lateral teeth. Internal genitalia simply convoluted.

DESCRIPTION: Medium to large, cribellate, web building spiders from 3-13 mm in length. Carapace pale to dark grey-brown, darkest anteriorly and with a more or less

Records of The Australian Museum, 1981, **Vol. 33 No. 18,** 779-802, Figures 1-46.

distinct basic colour pattern as follows: a patch of darker pigment in front of the fovea extending anteriorly along the margins of the caput; three lateral dark stripes radiating out from the fovea to the thoracic margins where they merge into a narrow marginal band. Dorsal surface of abdomen light to dark grey with a paler anterior mid-dorsal stripe usually flanked by similarly coloured patches plus several well-defined paired chevron markings posteriorly; ventral surface delimited by pale lateral lines. Legs banded. Colour pattern modified or absent in cave adapted species. Carapace with a well-defined caput. Fovea a long slit, broadening anteriorly. Eight eyes or none. Eye diameters: ALE⩾PME⩾PLE>AME. From above, the anterior eye row recurved, the posterior eye row straight or slightly procurved. Chelicerae vertical, with well developed boss. Two well separated, or three to five, retromarginal teeth; five to eight promarginal teeth, the basal three of which always consist of a medium sized inner tooth followed by a large tooth and a very small tooth. Sternum longer than wide with a slender prolongation between coxae IV. Maxillae parallel. Labium longer than wide, indented apically and basolaterally. Claw of female palp pectinate. Tibia of male palp with two apical processes, the ventral process a low, curved lamina, the retrolateral process broadly laminate basally with a curved spiniform extension apically. Embolus a long, slender, spiniform coil running around the margin of a broad, circular, membranous conductor. Retrolaterally, the conductor forks terminally to form two sclerotised processes, the anterior process typically a spiniform lamina, the posterior process typically spoon shaped. Median apophysis absent. Apical part of cymbium long or short, conical or attenuate. Legs long and slender, 1423 or 1243, with plumose and ciliate hairs. Trochanters slightly notched. Tarsi curved or straight. Trichobothria finely ciliate, in a single row on tarsus and metatarsus, two rows on tibia. Bothria collariform. Tarsal organ a small, round to oval opening, occasionally indented or with granular inclusions, placed on a low mound distal to trichobothria (fig. 46). **Typical leg spination.** — *Female:* LEG I, femur p0111, d222, tibia p111, r1111, d001, v222, metatarsus p1101, r1101, v221; LEG II, femur p1111, d2222, tibia p011, r111, d001, v222, metatarsus p112, r112, v221; LEG III, femur p1111, d2222, tibia p011, r111, d001, v222, metatarsus p112, d000, v221; LEG IV, femur p1101, d11122, tibia p011, r111, d001, v222, metatarsus p1112, r1012, v221. *Male:* LEG I, femur p1111, d2222, tibia p0111, r1111, v222, metatarsus p1102, r1101, v221; LEG II, femur p1111, d2222, tibia p011, r111, d001, v222; metatarsus p112, r112, v221; LEG III, femur p1111, d2222, tibia p011, r111, d01, v222, metatarsus p 112, r112, v221; LEG IV, femur p1101, d1122, tibia p011, r111, d01, v222, metatarsus p1112, r1012, d000, v221. Three claws, all toothed. Claw tufts or tenent hairs absent. Calamistrum subcentral. Abdominal hair ciliate. Epigynum variably sclerotised, raised, with a very shallow or deeply invaginated median fossa which is commonly obscured by posteriorly directed hairs. Lateral teeth absent. Internal genitalia with spermathecal ducts either short or simply convoluted. Anterior spinnerets broad at base, short, conical and contiguous. Posterior spinnerets longer and more slender with a conical terminal joint. Cribellum wide, bipartite, the spinning fields separated by a broad sclerotised septum expanding into a posterior sclerotised border. Cribellum spigots strobilate. Tracheal spiracle just in front of cribellum. Tracheal system simple with four unbranched tubes confined to abdomen.

TYPE SPECIES: *Baiami volucripes* (Simon 1908).

## KEY TO SPECIES OF *BAIAMI*

### FEMALES

1. Epigynum with a deeply excavated median fossa; sclerotisation weak or well developed only behind fossa. Internal ducts coiled (*glenelgi* species group) . 2

— Epigynum lacking a deeply excavated median fossa; epigynum strongly sclerotized. Internal ducts not coiled (*tegenarioides* species group) ............ 6

2. Internal ducts singly coiled ............ 3

— Internal ducts doubly coiled ............ *B. volucripes*

3. Posterior border of epigynal fossa strongly sclerotised. Internal ducts loosely coiled and converging from epigynal fossa ............ 4

— Posterior border of epigynal fossa weakly sclerotised. Internal ducts tightly coiled and diverging from epigynal fossa ............ 5

4. Sclerotised posterior border of fossa narrow, about one fifth as long as wide ............ *B. loftyensis*

— Sclerotised posterior border of fossa broad, more than one third as long as wide ............ *B. torbayensis*

5. Epigynal fossa large, anteriorly placed ............ *B. glenelgi*

— Epigynal fossa small, centrally placed ............ *B. montana*

6. Strongly pigmentated. 6 promarginal teeth. Spermathecae not lobed. Legs of moderate length. Metatarsus III with dorsal spines ............ *B. brockmani*

— Pigmentation often reduced. 5 promarginal teeth. Spermathecae deeply lobed. Legs long. Metatarsus III lacking dorsal spines ............ *B. tegenarioides*

MALES

1. Apical part of palpal tibia straight. Origin of embolus apical-lateral. Basal processes on cymbium lacking (*glenelgi* species group) ............ 2

— Apical part of palpal tibia flexed ventrally. Origin of embolus basal. Retrolateral process often present on basal part of cymbium (*tegenarioides* species group). 7

2. Embolus consisting of a single coil ............ 3

— Embolus consisting of a double coil ............ *B. volucripes*

3. Apical part of cymbium longer than basal part. Palpal tibia long ............ 4

— Apical part of cymbium shorter than basal part. Palpal tibia very short ...*B. stirlingi*

4. Anterior conductor process 7-9 times longer than wide, directed apically or laterally ............ 5

— Anterior conductor process attenuate, about 14 times longer than wide, directed basally ............ *B. glenelgi*

5. Anterior margin of conductor straight, anterior process directed laterally ............ *B. loftyensis*

— Anterior margin of conductor gently curved, anterior process sloping apically 6

6. Embolic duct visible on tegulum ............ *B. montana*

— Embolic duct not visible on tegulum ............ *B. torbayensis*

7. Basal process on cymbium lacking. Spiniform extension on retrolateral tibial process slender and finely pointed. Pigmentation normal ................*B. brockmani*

— Basal process present on cymbium. Spiniform extension on retrolateral tibial process thick and bluntly pointed. Pigmentation often reduced or lacking.... 8

8. Eyes normal, pigmentation often reduced .................................*B. tegenarioides*

— Eyes absent, pigmentation lacking.....................................*B. mullamullangensis*

REMARKS: Spination data given in species descriptions indicate differences from generic pattern only. Body size data is given as a range for the smallest and largest mature specimens in each species sample. All types are lodged in the Australian Museum, Sydney unless otherwise noted.

### **Baiami glenelgi** n. sp.

Figs. 11, 18, 34, 39

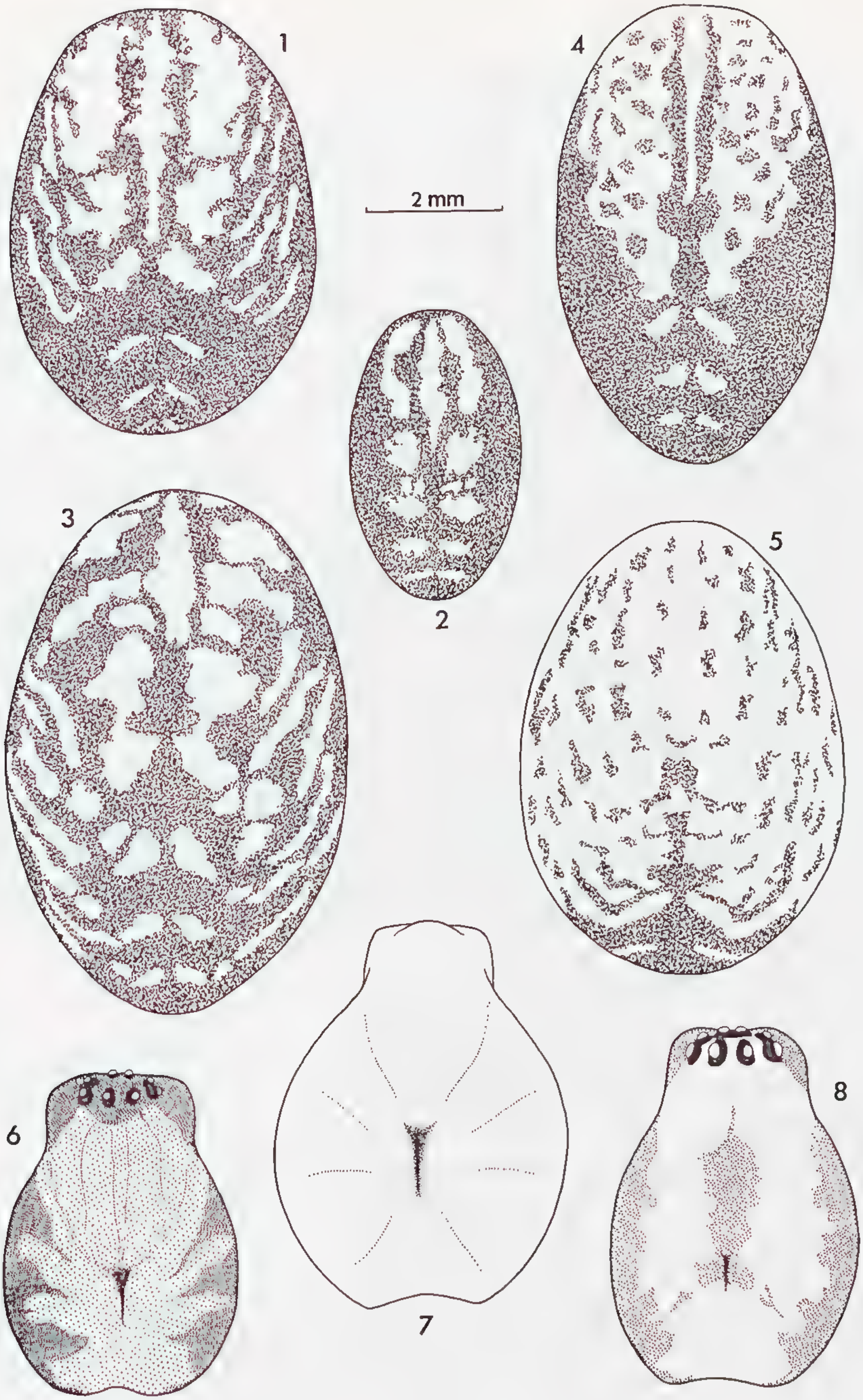
FEMALE: Dimensions (mm). — Carapace length 4.78-4.92; width 3.34-3.43. Abdomen length 6.12-6.38; width 4.15-4.25. Colour — Carapace dark greyish brown, otherwise as for genus. Abdomen dark grey with a narrow, pale mid dorsal stripe flanked by well defined pale brown lateral patches and posterior chevron markings. Ventral surface grey, bounded laterally by paler stripes, with several pale spots in front of spinnerets. *Eyes* — Diameters (mm): AME 0.15; ALE 0.21; PLE 0.17; PME 0.18. Interdistances (mm): AME-AME 0.11; AME-ALE 0.17; ALE-PLE 0.11; PLE-PME 0.28; PME-PME 0.25. M.O.Q. (mm): posterior width 0.61; anterior width 0.41; length 0.61. Clypeus height 2.2 diameters of an AME. Cheliceral teeth — Retromargin, 2 widely separated; Promargin, 7-8. *Legs* — 1243. Tarsi straight. Spination. LEG I: femur p1111; metatarsus p1102. LEG II: tibia p0111, r1111. LEG III: femur d12222. *Female genitalia* — Epigynum weakly sclerotised. Fossa opening large, transversely oval, anteriorly placed. Internal posterior extension of fossa long and placed well in front of the spermathecae to which it is joined by broad ducts coiled closely once around the front of the spermathecae. Ducts diverge from fossa. Spermathecae in contact in the midline.

MALE: Dimensions (mm). — Carapace length 4.81-5.20; width 3.46-3.81. Abdomen length 4.32-4.53; width 2.90-3.30. *Eyes* — Diameters (mm): AME 0.13; ALE 0.20; PLE 0.16; PME 0.16. Interdistances (mm): AME-AME 0.11; AME-ALE 0.15; ALE-PLE 0.09; PLE-PME 0.21; PME-PME 0.23. M.O.Q. (mm): posterior width 0.55; anterior width 0.37; length 0.57. Clypeus height 3.0 diameters of an AME. *Legs* — Spination: LEG I, femur r0010, tibia v2212; LEG IV, femur d11122, metatarsus d001. *Male palp* — Cymbium length-width ratio 2.4:1, without basal processes; apical part conical, not dorsally flexed, longer than basal part. Origin of embolus subcentral on retrolateral side. Embolic duct visible on tegulum. Embolus makes almost a complete turn from origin, terminating on anterior conductor process. Terminal processes of conductor subapical to central on retrolateral side. Anterior process elongate, slender, spiniform (longer than wide in ratio 14:1), directed basally; posterior process slender, spoon shaped. Tibia eight times as long as wide and only slightly longer than patella. Retrolateral tibial process with a long, slender, spiniform extension, directed apically.

HOLOTYPE FEMALE: KS 1683 — Glenelg River, nr Dartmoor, Vic. 25.iii.1974. M. Gray.

PARATYPES: KS 1681 and KS 1682 — males, Glenelg River, nr. Dartmoor, Vic. 26. iii. 1974, M. Gray. KS 1684 — Female, Glenelg River, nr. Dartmoor, Vic. 25. iii. 1974, M. Gray.

RECORDS: KS 1726 — Juv., Zumsteins, Grampian Ra., Vic. 3.v.1973, M. Gray.



Figs. 1-8. Dorsal views of abdomen (Fig. 1-5) and carapace (Fig. 6-8). Figs. 1, 2, 3 and 6 are representative of typical 'basic colour patterns' in the genus. 1, *Baiami brockmani,* female. 2, *B. volucripes,* male. 3, *B. torbayensis,* female. 4, *B. montana,* female. 5, *B tegenarioides,* female. 6, *B. volucripes,* female. 7, *B. mullamullangensis,* penult. juvenile. 8, *B. tegenarioides,* female.

### **Baiami loftyensis** n. sp.

Figs. 9, 20, 29, 36

FEMALE: Dimensions (mm) — Carapace length 5.91; width 4.25. Abdomen length 4.90; width 3.42. Colour — Carapace dark grey-brown, otherwise as for genus. Abdomen dark grey with a pale narrow mid-dorsal stripe flanked laterally by brownish patches with paler chevron markings posteriorly. Ventral abdomen grey bounded laterally by pale stripes, with several pale spots centrally. *Eyes* — Diameters (mm): AME 0.14; ALE 0.24; PLE 0.17; PME 0.19. Interdistances (mm): AME-AME 0.15; AME-ALE 0.25; ALE-PLE 0.11; PLE-PME 0.28; PME-PME 0.25. M.O.Q. (mm): posterior width 0.63; anterior width 0.43; length 0.69. Clypeus height 3.2 diameters of an AME. Cheliceral teeth — Retromargin, 2 widely separated; Promargin, 6-8. *Legs* — 1423. Tarsi straight. Spination: LEG I, femur p1(weak)111, tibia d000, metatarsus v220; LEG II, metatarsus p111, r111; LEG IV, femur d1122. *Female genitalia* — Epigynum with a narrow, strongly sclerotized transverse border behind the anteriorly sited ovoid fossa. Internal posterior extension of fossa short and broad, connected to the spermathecae by thin ducts which curve toward each other between the widely separated spermathecae and then coil loosely once around them.

MALE: Dimensions (mm) — Carapace length 5.02-5.12; width 3.70-3.75. Abdomen length 4.90-5.50; width 3.12-3.80. *Eyes* — Diameters (mm): AME 0.12; ALE 0.19; PLE 0.17; PME 0.18. Interdistances (mm): AME-AME 0.11; AME-ALE 0.19; ALE-PLE 0.04; PLE-PME 0.23; PME-PME 0.17. M.O.Q. (mm): posterior width 0.53; anterior width 0.35; length 0.58. *Legs* — Spination: LEG I, metatarsus r1102; LEG IV, metatarsus d001. *Male palp* — cymbium length-width ratio 2.6:1, basal processes lacking; apical part conical, not dorsally flexed, longer than basal part. Origin of embolus central on retrolateral side. Embolic duct visible on tegulum. Embolus makes a complete turn from origin, terminating on anterior conductor process. Anterior border of conductor straight. Terminal processes of conductor apical on retrolateral side. Anterior process long, triangular, spiniform (longer than wide in ratio 7:1), directed laterally; posterior process spoon shaped, very shallow. Tibia eight times longer than wide and only slightly longer than patella. Retrolateral tibial process with a long, slender, spiniform extension, directed apically.

HOLOTYPE FEMALE: KS 1687 — Cleland Conserv. Res., Sthn. Mt. Lofty Ra., S.A. 11.iv.1973, M. Gray.

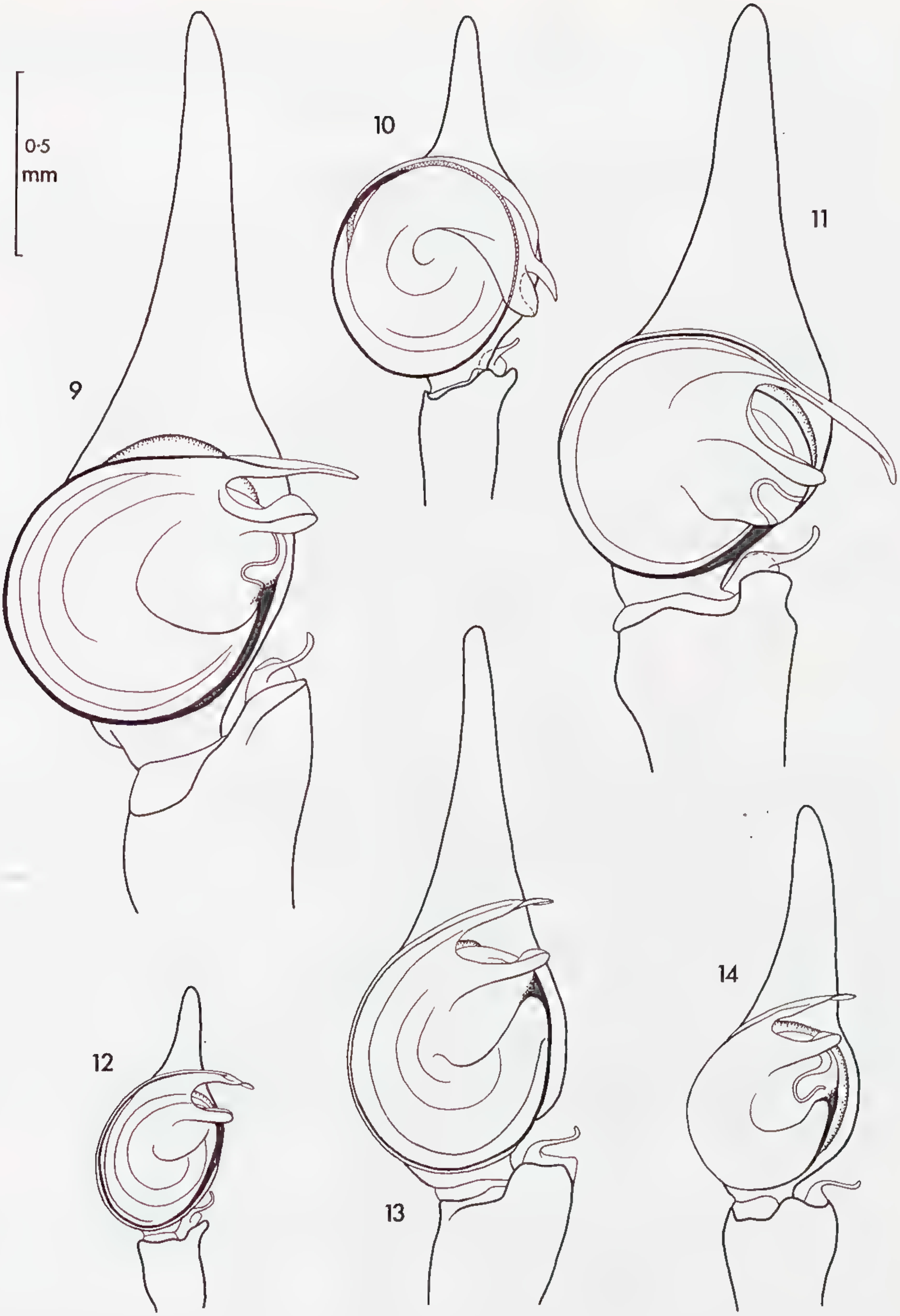
PARATYPES: KS 1685 — Male, Morialta Nat. Pk., Sthn. Mt. Lofty Ra., S.A., 15.iv.1973, M. Gray. KS 1686 — Male, Cleland Conserv. Res., Sthn. Mt. Lofty Ra., S.A., ii. 1973, M. Gray.

RECORDS: KS 1690 — Juv., Hahndorf, Sthn. Mt. Lofty Ra., S.A., Dec. 1908.

### **Baiami torbayensis** n. sp.

Figs. 3, 13, 21, 30, 37

FEMALE: Dimensions (mm) — Carapace length 5.17; width 3.37. Abdomen length 6.70; width 4.75. Colour — Carapace grey-brown, otherwise as for genus. Abdomen brown with a narrow pale mid-dorsal stripe flanked by pale grey patches with paler chevron markings posteriorly which tend to merge laterally. Ventral abdomen orange-brown with four pale parallel stripes running from genital fold almost to spinnerets. *Eyes* — Diameters (mm): AME 0.14; ALE 0.19; PLE 0.17; PME 0.19. Interdistances (mm): AME-AME 0.09; AME-ALE 0.14; ALE-PLE 0.12; PLE-PME 0.26; PME-PME 0.26. M.O.Q. (mm): posterior width 0.64; anterior width 0.37; length 0.65. Clypeus height 2.78 diameters of AME. Cheliceral teeth — Retromargin, 2 widely separated; Promargin, 6. *Legs* — 1423. Tarsi curved. Spination: LEG IV, femur d111122,



Figs. 9-14 Male palp (*glenelgi* species group), palpal organ, distal tibia, ventral. 9, *B. loftyensis*. 10, *B. volucripes*. 11, *B. glenelgi*. 12, *B. stirlingi*. 13, *B. torbayensis*. 14, *B. montana*.

tibia v112. *Female genitalia* — Epigynum with a broad sclerotised border enclosing the transversely ovoid opening of the fossa posterolaterally. Fossa deep but without internal posterior extension, leading into broad ducts which curve inwards towards the midline, then coil loosely once around the frontal aspects of the spermathecae. Spermathecae in contact anteriorly.

MALE: Dimensions (mm) — Carapace length 4.59; width 3.31. Abdomen length 4.30; width 2.70. *Eyes* — Diameters (mm): AME 0.14; ALE 0.19; PLE 0.16; PME 0.19. Interdistances (mm): AME-AME 0.07; AME-ALE 0.14; ALE-PLE 0.07; PLE-PME 0.16; PME-PME 0.20. M.O.Q. (mm): Posterior width 0.58; anterior width 0.35; length 0.59. Clypeus height 2.14 diameters of an AME. *Legs* — Spination: LEG I, tibia p1111, metatarsus r1102; LEG IV, femur d111122. *Male palp* — Cymbium length-width ratio 2.5:1, basal processes lacking; apical part conical, not dorsally flexed, longer than basal part. Origin of embolus subapical on retrolateral side. Embolic duct not visible on tegulum. Embolus makes a complete turn from origin, terminating on anterior conductor process. Terminal processes of conductor apical. Anterior process long, triangular, spiniform (longer than wide in ratio 7:1), directed apically; posterior process spoon shaped. Tibia eight times longer than wide, longer than patella in ratio 1.3:1. Retrolateral tibial process with a long slender spiniform extension, directed apically.

HOLOTYPE FEMALE: KS 1671 — Torbay Head, nr. Albany, W.A. 15.i.1975, B. Y. Main.

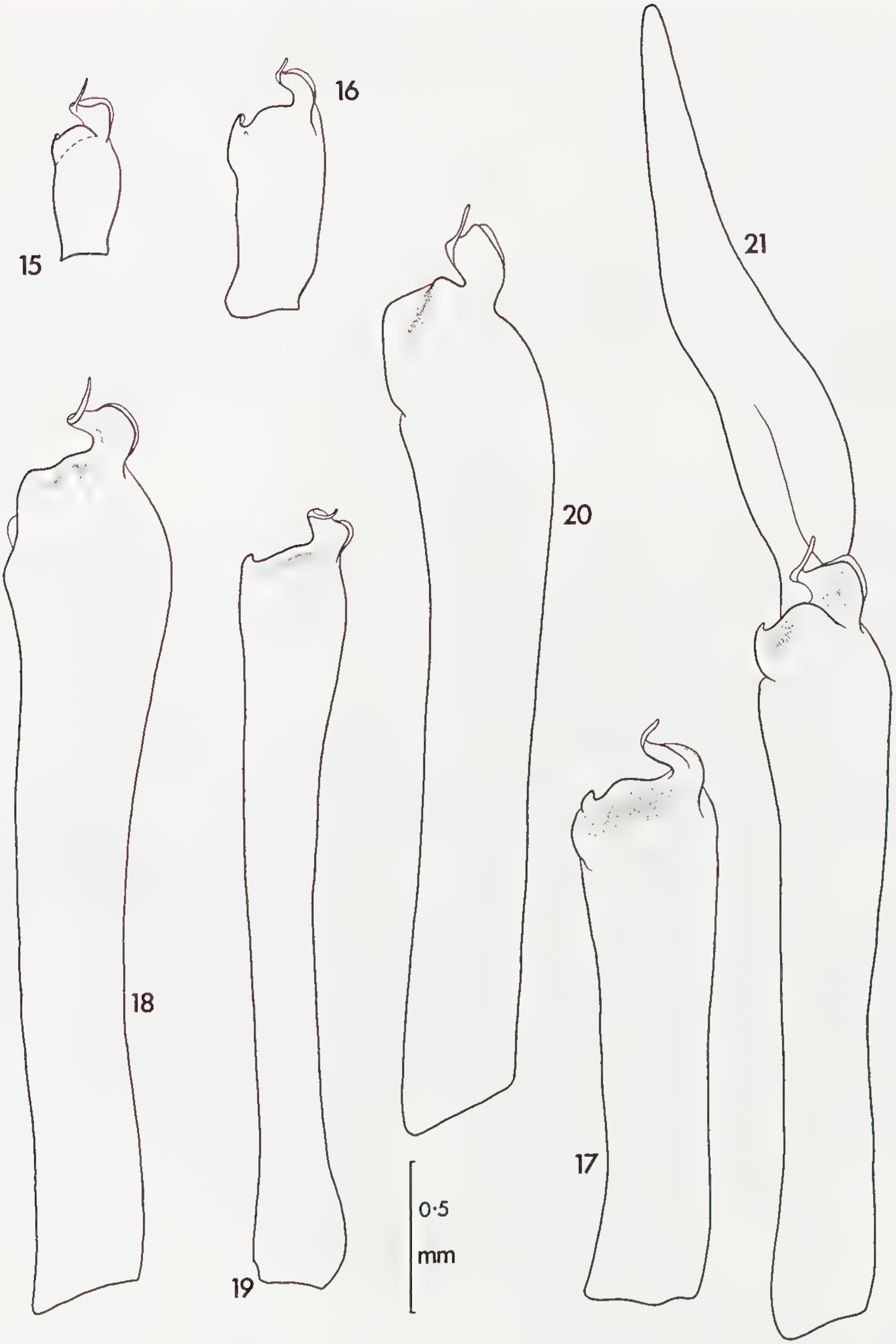
PARATYPES: KS 1670 — Male, Torbay Head, nr. Albany, W.A., 15.i.1975, B. Y. Main. KS 3105 — Male and Female, Two People Bay Nat. Pk., nr. Albany, W.A., Feb. 1979, M. Gray.

## **Baiami montana** n. sp.

Figs. 4, 14, 19, 33, 38; 46.

FEMALE: Dimensions (mm) — Carapace length 3.88-4.75; width 2.80-3.22. Abdomen length 5.39-5.70; width 3.20-4.20. Colour — Carapace dark grey-brown, otherwise as for genus. Abdomen dark grey posteriorly, lighter grey spotting anteriorly with a narrow pale mid-dorsal stripe flanked by pale brownish patches followed by several paler chevron markings posteriorly. Ventral surface grey with four pale parallel stripes running between genital fold and spinnerets. *Eyes* — Diameters (mm): AME 0.16; ALE 0.20; PLE 0.17; PME 0.19. Interdistances (mm): AME-AME 0.09; AME-ALE 0.16; ALE-PLE 0.11; PLE-PME 0.21; PME-PME 0.25. M.O.Q. (mm): posterior width 0.63; anterior width 0.41; length 0.67. Clypeus height 2.12 diameters of an AME. Cheliceral teeth — Retromargin, 2 widely separated; Promargin, 6. *Legs* — 1423. Tarsi slightly curved. Spination: LEG II, femur p0111, tibia r1111; LEG IV, tibia p0111, r111, metatarsus r1112. *Female genitalia* — Epigynum small with a deep, rounded fossa, delimited posteriorly by a raised, weakly sclerotised border. Internal posterior extension of fossa narrow with ducts diverging from it to coil tightly once about the anterior aspect of spermathecae. Spermathecae slightly separated.

MALE: Dimensions (mm) — Carapace length 3.85-4.51; width 2.91-3.10. Abdomen length 4.05-4.42; width 2.42-2.80. *Eyes* — Diameters (mm): AME 0.14; ALE 0.21; PLE 0.16; PME 0.18. Interdistances (mm): AME-AME 0.05; AME-ALE 0.08; ALE-PLE 0.06; PLE-PME 0.18; PME-PME 0.19. M.O.Q. (mm): posterior width 0.54; anterior width 0.33; length 0.55. Clypeus height 1.25 diameters of an AME. *Legs* — Spination: LEG I, femur p0111, metatarsus p111, v202; LEG II, tibia d000; LEG IV, femur p10111, d2222, metatarsus p112. *Male palp* — Cymbium length-width ratio 2.4:1, without basal processes; apical part conical, not dorsally flexed, longer than basal part. Origin of embolus central on retrolateral side. Embolic duct visible on tegulum. Embolus makes a three quarter turn



Figs. 15-21 Male palp, (*glenelgi* species gp.) tibia, retrolateral. 15, *B. stirlingi*. 16 and 17, *B. volucripes*. 18, *B. glenelgi*. 19, *B. montana*. 20, *B. loftyensis*. 21, *B. torbayensis*, tibia and cymbium.

from origin, terminating on anterior conductor process. Terminal processes of conductor apical. Anterior process long, triangular, spiniform (longer than wide in ratio 9:1), directed apically; posterior process spoon shaped. Tibia ten times as long as wide and only slightly longer than patella. Retrolateral tibial process with a long, slender, spiniform extension, directed dorsally.

HOLOTYPE FEMALE: KS 1697 — Castle Rock Trail, Porongorup Range Nat. Pk., W.A., 16.i.1974, M. Gray.

PARATYPES: KS 3157 — Males, Castle Rock Trail, Porongorup Range Nat. Pk., W.A., Feb. 1979, M. Gray. KS 3158 — Female, White Gum Flat Fire Trail, Stirling Range Drive, Stirling Range Nat. Pk., W.A., Feb. 1979, M. Gray. KS 3159 — Male, White Gum Flat Fire Trail, Stirling Range Drive, Stirling Range Nat. Pk., W.A., Feb. 1979, M. Gray.

RECORDS: KS 3163 — Male and Female, Hayward Trail, Bolganup Rd., Porongorup Range Nat. Pk., W.A., Feb. 1979, M. Gray.

### **Baiami stirlingi** n. sp.

Figs. 12, 15

MALE: Dimensions (mm) — Carapace length 1.66; width 1.36. Abdomen length 1.51; width 1.03. Colour — Carapace grey-brown, otherwise as for genus. Abdomen grey with pale mid-dorsal stripe flanked by brownish patches behind which are several large pale chevron markings. Ventral abdomen grey with paler lateral lines and indistinctly limited pale patches centrally. *Eyes* — Diameters (mm): AME 0.07; ALE 0.10; PLE 0.09; PME 0.09. Interdistances (mm); AME-AME 0.04; AME-ALE 0.05; ALE-PLE 0.03; PLE-PME 0.07; PME-PME 0.11. M.O.Q. (mm): posterior width 0.29; anterior width 0.18; length 0.28. Clypeus height 1.5 diameters of an AME. Cheliceral teeth — Retromargin, 2 widely separated; Promargin, 5. *Legs* — 1423. Tarsi curved. Spination: LEG I, femur p0011, d1111, tibia p001, metatarsus p011, r001; LEG II, femur p011, d1111; tibia r101, v02, metatarsus p012, r011; LEG III, femur p011, d1111, tibia r101, v01; LEG IV, femur p001, d111121, tibia v12. *Male palp* — Cymbium length-width ratio 2.1:1, basal processes lacking; apical part conical, not dorsally flexed, shorter than basal part. Origin of embolus subapical on retrolateral side. Embolic duct not visible on tegulum. Embolus makes a complete turn from origin, terminating on anterior conductor process. Terminal processes of conductor apical on retrolateral side. Anterior process long, triangular, spiniform (longer than wide in ratio 6.75:1), directed laterally; posterior process slender, spoon shaped. Tibia longer than wide in ratio 2.3:1 and shorter than patella in ratio 0.9:1. Retrolateral tibial process with a long, slender spiniform extension, directed apically.

HOLOTYPE MALE: KS 1699 — White Gum Flat Fire Trail, Stirling Range Drive, Stirling Range Nat. Pk., W.A., 15.i.1974, M. Gray.

PARATYPE: KS 3160 — male, locality as for holotype, Feb. 1979, M. Gray.

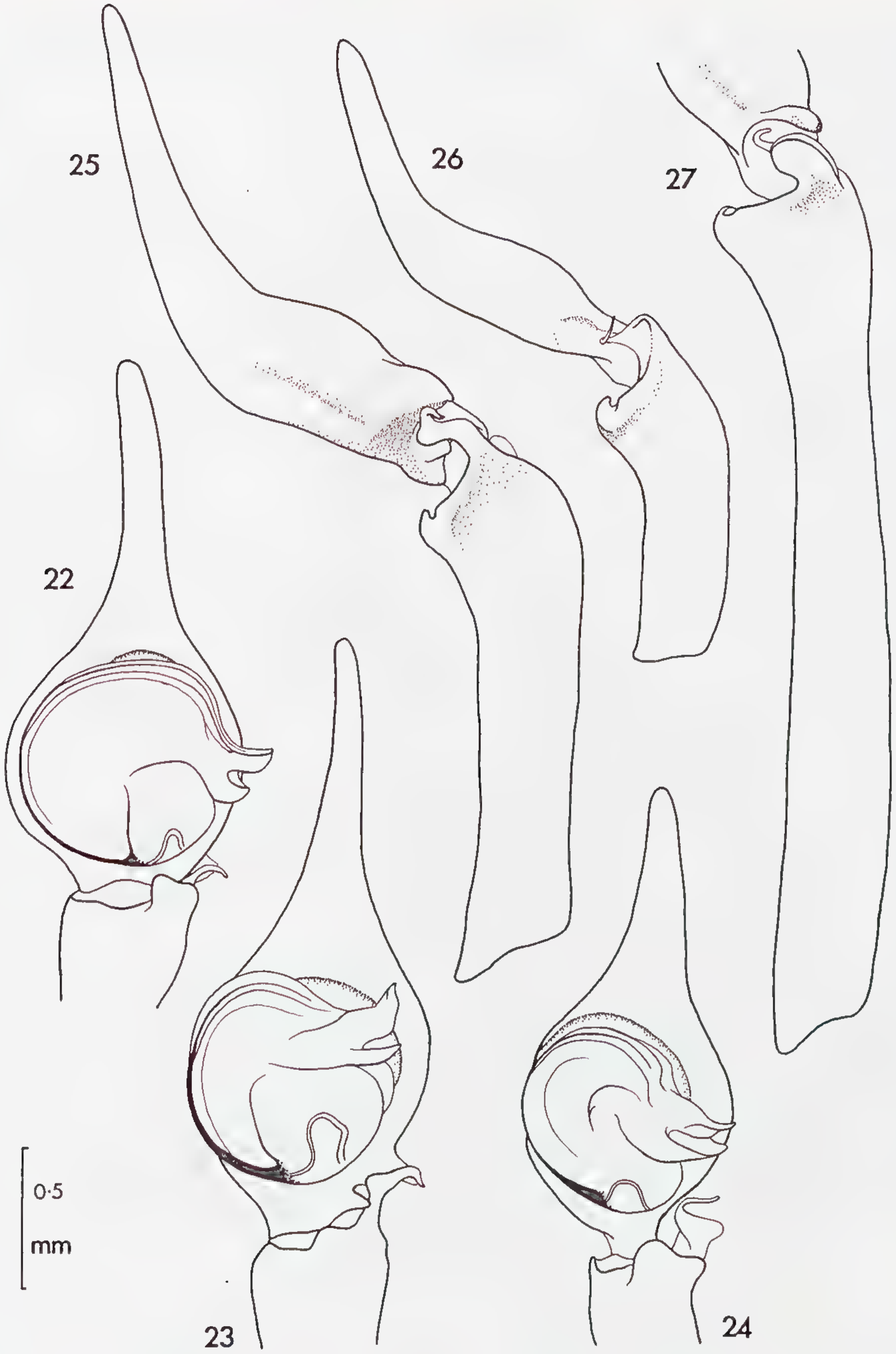
### **Baiami volucripes** (Simon, 1908)

Figs. 2, 6, 10, 16, 17, 31, 32, 41, 46

*Epimecinus volucripes* Simon, 1908: 377

*Baiami volucripes* Lehtinen, 1967: 218

FEMALE: Dimensions (mm) — Carapace length 3.02-4.75; width 2.26-3.84; Abdomen length 3.50-5.20; width 2.40-4.25. Colour — Carapace grey-brown, otherwise as for genus. Abdomen greyish overall with a paler mid dorsal stripe flanked by pale brownish



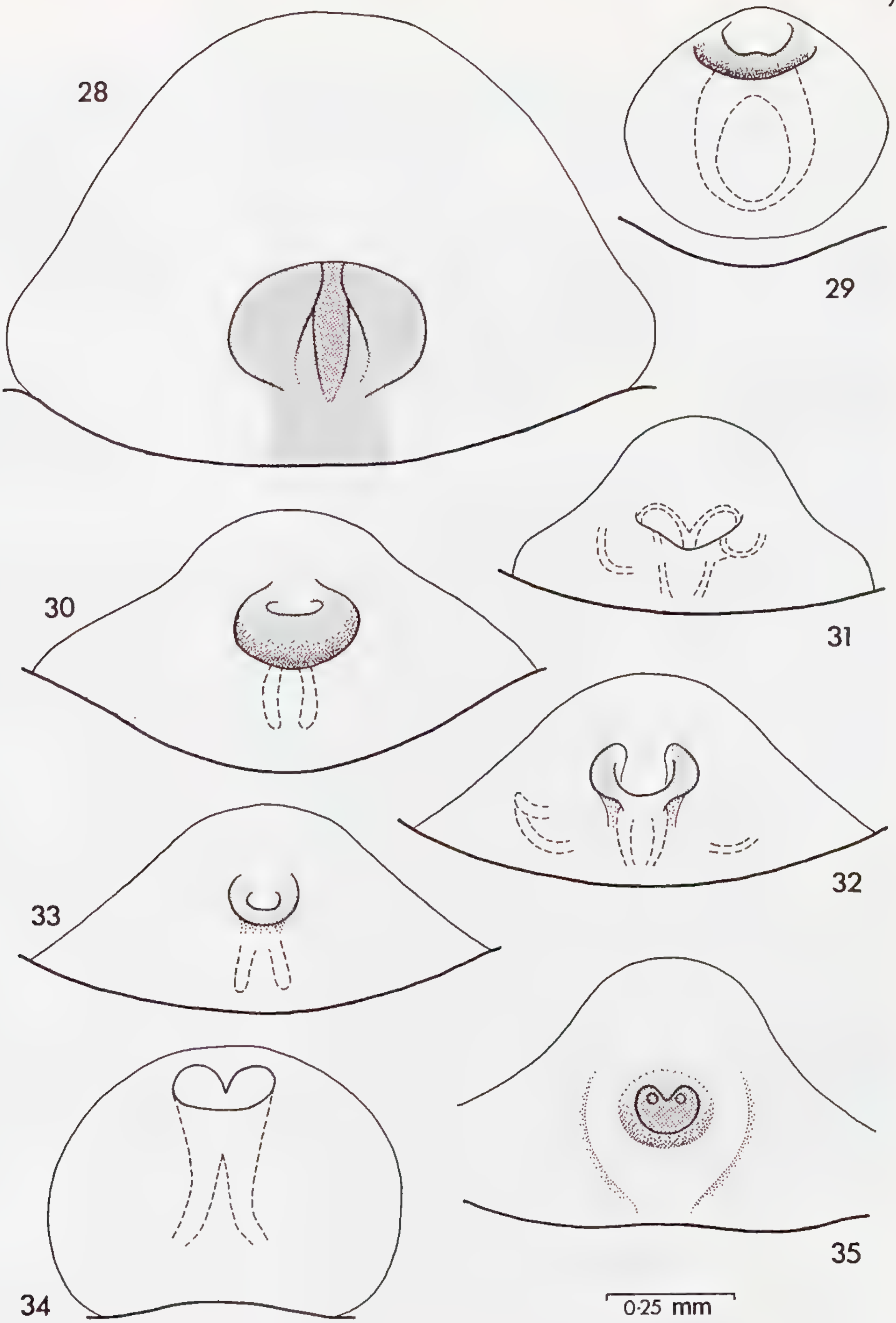
Figs. 22-27. Male palp (*tegenarioides* species gp.) Figs. 22-24: palpal organ, distal tibia, ventral, 22, *B. mullamullangensis*. 23, *B. tegenarioides*. 24, *B. brockmani*. Figs. 25-27, tibia and cymbium, retrolateral; 25, *B. tegenarioides*. 26, *B. brockmani*. 27. *B. mullamullangensis*.

areas and followed by several pale chevron markings. Ventral abdomen light grey, bounded on each side by paler lines with two less distinct parallel lines centrally. *Eyes* — Diameters (mm): AME 0.11; ALE 0.18: PLE 0.16: PME 0.16. Interdistances (mm): AME-AME 0.11; AME-ALE 0.20; ALE-PLE 0.09; PLE-PME 0.25; PME-PME 0.26. M.O.Q. (mm): posterior width 0.58; anterior width 0.33; length 0.55. Clypeus height 3.27 diameters of an AME. Cheliceral teeth — Retromargin, 2 widely separated; Promargin, 6. *Legs* — 1423. Tarsi straight. Spination: LEG I, tibia v122, metatarsus p0101, r0101, v220; LEG II, tibia v122, metatarsus r012; LEG III, tibia v212. *Female genitalia* — Epigynum weakly sclerotised with raised, swollen posterolateral border around opening of the large, centrally placed fossa. Fossa deep, internal posterior extension short, leading into slender ducts coiled twice around the frontal region of the spermathecae. Spermathecae in contact in midline.

MALE: Dimensions (mm) — Carapace length 2.54-4.00; width 1.72-3.05. Abdomen length 1.85-3.35; width 0.87-2.05. *Eyes* — Diameters (mm): AME 0.09; ALE 0.14; PLE 0.11; PME 0.12. Interdistances (mm): AME-AME 0.05; AME-ALE 0.08; ALE-PLE 0.04; PLE-PME 0.11; PME-PME 0.12. M.O.Q. (mm): posterior width 0.36; anterior width 0.23; length 0.37. Clypeus height 1.33 diameters of an AME. *Legs* — Spination: LEG I, tibia r111, v122, metatarsus v220; LEG III, femur p1111. *Male palp* — Cymbium length-width ratio 1.6:1, without basal processes apical part conical, weakly dorsally flexed, shorter than basal part. Conductor large, circular. Origin of embolus central to subapical on prolateral side. Embolic duct not visible on tegulum. Embolus makes one and a half turns from origin, terminating on anterior conductor process. Terminal processes of conductor placed centrally-subbasally on retrolateral side. Anterior process short, curved, spiniform (longer than wide in ratio 3.5:1), directed basally; posterior process broad, spoon shaped. Conductor margin slightly indented distally. Tibia three to five times as long as wide and equal to or slightly longer than patella. Retrolateral tibial process with a slender spiniform extension, directed apically.

TYPES: National Museum, Paris — Female, AR 387, Southwestern Australia, 1905, W. Michaelsen and R. Hartmeyer. Zoological Museum, Berlin — Juveniles, ZMB 13841, Rottnest, ZMB 13842 and 13843 Jarrahdale, ZMB 13844, Pickering Brook, Southwestern Australia, 1905, W. Michaelsen and R. Hartmeyer. Zoological Institute and Zoological Museum, Hamburg — specimens (not seen) from Jarrahdale and Rottnest, Southwestern Australia, 1905, W. Michaelsen and R. Hartmeyer.

RECORDS: KS 1711 — Male and female, Jarrahdale, 12.6km E., nr. creek beyond Arboretum Road T.O. on Balmoral Road, W.A., 24.xii. 1973, M. Gray. KS 1712 — Male and female, Regan's Ford, Moore R., W.A., 26.xii.1973, M. Gray. KS 1713 — Male and female, Stirling Ra., White Gum Flat Fire Trail, Stirling Ra. Drive, W.A., 15.i.1974, M. Gray. KS 1714 — Male, Bridgetown, W.A., M. Gray. KS 3103 — Male, Boranup Drive, N.W. of Karridale, W.A., Feb. 1979, M. Gray. KS 1715 — Juv., 9.6km E. of Mundaring Weir, W.A., 28.xii.1973, M. Gray. KS 1716 — Male and juv., Mundaring, W.A., 5.xi.1971, J. A. Springett. KS 1717 — Juv., Gleneagle, W.A., 1971, J. A. Springett. KS 1718 — Male and female, Un-named Cave, SH20, Nambung Nat. Pk., nr. Cervantes, W.A., 23.ii.1974, J. W. J. Lowry. KS 1719 — Female and juv., Unnamed Cave, Nambung Nat. Pk., nr. Cervantes, W.A., 23.ii.1974, J. W. J. Lowry. KS 1720 — Female, Echnida Cave, SH51, Nambung Nat. Pk., nr. Cervantes, W.A., 23.ii.1974, J. W. J. Lowry. KS 1722 — Male, Census Cave, Main Chamber nr. Yanchep, W.A., 22.viii.1965, B. Muir. KS 1723 — Juv., Census Cave, nr. Yanchep, W.A., 22.viii.1966, B. Muir. 74/6 (W.A. Mus. coll.) — Juv., Yanchep area, in cave, W.A., 22.i.1912, Bennett and Baynes. BS 1596 (S.A. Mus. coll.) — Juv., Yanchep Cave, Yanchep, W.A., 7.v.1967, E. Hamilton Smith. BS 2122 (S.A. Mus. coll.) — Juv., Unnamed Cave, SH5, Nambung R., W.A., 19.v.1973, R. Shoosmith. BS 1590 (S.A. Mus. coll.) — Juv., Mambiddy Cave, Yanchep, W.A., 7.v.1967, E. Hamilton Smith.



Figs. 28-35. Female external genitalia. 28, *B. tegenarioides*. 29, *B. loftyensis*. 30, *B. torbayensis*. 31, *B. volucripes*, TYPE. 32, *B. volucripes*. 33, *B. montana*. 34, *B. glenelgi*. 35, *B. brockmani*.

### **Baiami brockmani** n. sp.

Figs. 1, 24, 26, 35, 40

FEMALE: Dimensions (mm) — Carapace length 3.80-5.75; width 2.59-3.85. Abdomen length 3.60-7.00; width 2.65-4.20. Colour — Carapace dark grey-brown, otherwise as for genus. Abdomen dark grey-brown with a narrow, pale mid-dorsal stripe flanked anteriorly by pale brown patches with several distinct chevron markings posteriorly. Ventral abdomen grey, delimited by paler stripes laterally, with indistinct paler markings centrally, most noticeably a pair of white spots behind the epigynal fold. *Eyes* — Diameters (mm): AME 0.12; ALE 0.21; PLE 0.16; PME 0.17. Interdistances (mm): AME-AME 0.12; AME-ALE 0.29; ALE-PLE 0.11; PLE-PME 0.37; PME-PME 0.30. M.O.Q. (mm): posterior width 0.64; anterior width 0.36; length 0.66. Clypeus height 3.54 diameters of an AME. Cheliceral teeth — Retromargin, 2 widely separated; Promargin, 6. *Legs* — 1423. Tarsi slightly curved. Spination: LEG I, metatarsus r0101; LEG II, tibia p1111, r0101; LEG III, metatarsus d010; LEG IV, femur d1122, metatarsus r102. *Female genitalia* — Epigynum a small, circular, strongly sclerotised plate. Fossa a slight indentation only, the paired openings of the spermathecal ducts visible laterally. Ducts short and broad, not coiled. Spermathecae elongate, in contact in midline.

MALE: Dimensions (mm) — Carapace length 3.05-4.60; width 2.37-3.42. Abdomen length 2.00-4.60; width 1.60-3.55. *Eyes* — Diameters (mm): AME 0.10; ALE 0.17; PLE 0.14; PME 0.15. Interdistances (mm): AME-AME 0.12; AME-ALE 0.17; ALE/PLE 0.10; PLE-PME 0.26; PME-PME 0.25. M.O.Q. (mm): posterior width 0.55; anterior width 0.32; length 0.52. Clypeus height 3.12 diameters of an AME. *Legs* — Spination: LEG I, tibia r1011, metatarsus r1102; LEG II, femur p0111, metatarsus r012. *Male palp* — Cymbium length-width ratio 2:1, without basal processes; apical part conical, strongly flexed dorsally, as long as basal part. Origin of embolus basal. Embolic duct visible on tegulum. Embolus makes a half turn from origin, terminating proximal to anterior conductor process. Terminal processes of conductor placed centrally on retrolateral side. Anterior process broad, triangular, spiniform (2.5 times longer than basal width), directed laterally; posterior process broad, spoon shaped. Conductor margin indented distally, anterior process set at obtuse angle to it. Tibia four times as long as wide and half as long as patella. Head of tibia flexed ventrally. Retrolateral tibial process with a long, slender, spiniform extension, directed anteriorly.

HOLOTYPE FEMALE: KS 1693 — Brockman Nat. Pk., nr. Pemberton, W.A., 22.i.1974, M. Gray.

PARATYPES: KS 1692 — Male, Pemberton, W.A., 1971, J. A. Springett. KS 1694 — Male, Brockman Nat. Pk., nr. Pemberton, W.A., 22.i.1974, M. Gray. KS 3104 — Male and female, Hilltop Rd., Walpole-Nornalup Nat. Pk., W.A., Feb. 1979, M. Gray. *Records:* KS 1695 — Juv., Shannon, Sutton Block, W.A., 1971, J. A. Springett. KS 1696 — Juv., Shannon R., Nelson Rd., S. of Shannon, W.A., 22.i.1974, M. Gray. W. A. Mus. coll. — Female, Warren Nt. Pk., nr. Pemberton, W.A., 19.v.1970, J. A. Springett.

### **Baiami mullamullangensis** (Gray, 1973)

Figs. 7, 22, 27, 45, 46.

*Tartarus mullamullangensis* Gray, 1973: 211

MALE: Dimensions (mm) — Carapace length 5.58; width 4.29, cephalic region narrow, thoracic region subcircular. Abdomen length 5.90; width 4.30. Colour — pigmentation absent. Carapace pale amber, a little darker towards caput. Abdomen cream coloured. *Eyes* — absent. Cheliceral teeth — Retromargin, 3 to 5; Promargin, 6 to

7, all approximately equal in size. *Legs* — 1243, very long. Tarsi curved. Plumose hair abundant. Spination reduced and as follows: LEG I, femur p11111, d21112101, tibia v0101, metatarsus p1101, v2020 (irreg.); LEG II, femur p2(weak)111, d222101, tibia p0111, r1111, do, vo1110, metatarsus p1111, r1101; LEG IV, femur p1100, d21211, tibia p111, r11111, do, v010, metatarsus p1111, r1011, d20. *Male palp* — Cymbium length-width ratio 2.5:1. One basal process on dorsal retrolateral aspect of cymbium base. Apical part of cymbium very slender, digitiform,flexed dorsally and much longer than basal part. Origin of embolus basal. Embolic duct visible on tegulum. Embolus makes a three quarter turn from origin, terminating proximal toconductor processes. Terminal processes of conductor centrally placed on retrolateral side. Anterior process short, thick, spiniform (2 times as long as wide), directed laterally; posterior process a short, heavy spoon. Conductor margin indented distally, anterior process set at right angles to it. Tibia 9.5 times as long as wide and 1.5 times as long as patella. Head of tibia weakly flexed ventrally. Retrolateral tibial process with a mildly tapered, blunt, spiniform extension, curved dorsally.

HOLOTYPE MALE: BS 1860 (S.A. Mus. coll.) — Mullamullang Cave, N37 (Dome Chamber), Nullarbor Plain, nr. Madura, W.A., 10.i.1969, P. Hawkes.

PARATYPES: KS 0005 — Juv., Mullamullang Cave, N37 (Dome Chamber), Nullarbor Plain, W.A., 4.i.1972, G. Sjoberg and M. Gray. KS 0006 — Juv., Mullamullang Cave, N37 (Dome Chamber), Nullarbor Plain, W.A. 25.xii.1967, M. Gray and B. Muir.

RECORDS: KS 1724 — Juv. (exoskeleton only),Mullamullang Cave, N37 (The Sail), Nullarbor Plain, W.A., 21.vii.1977, G. Campbell.

### **Baiami tegenarioides** (Simon, 1908)

Figs. 5, 8, 23, 25, 28, 42

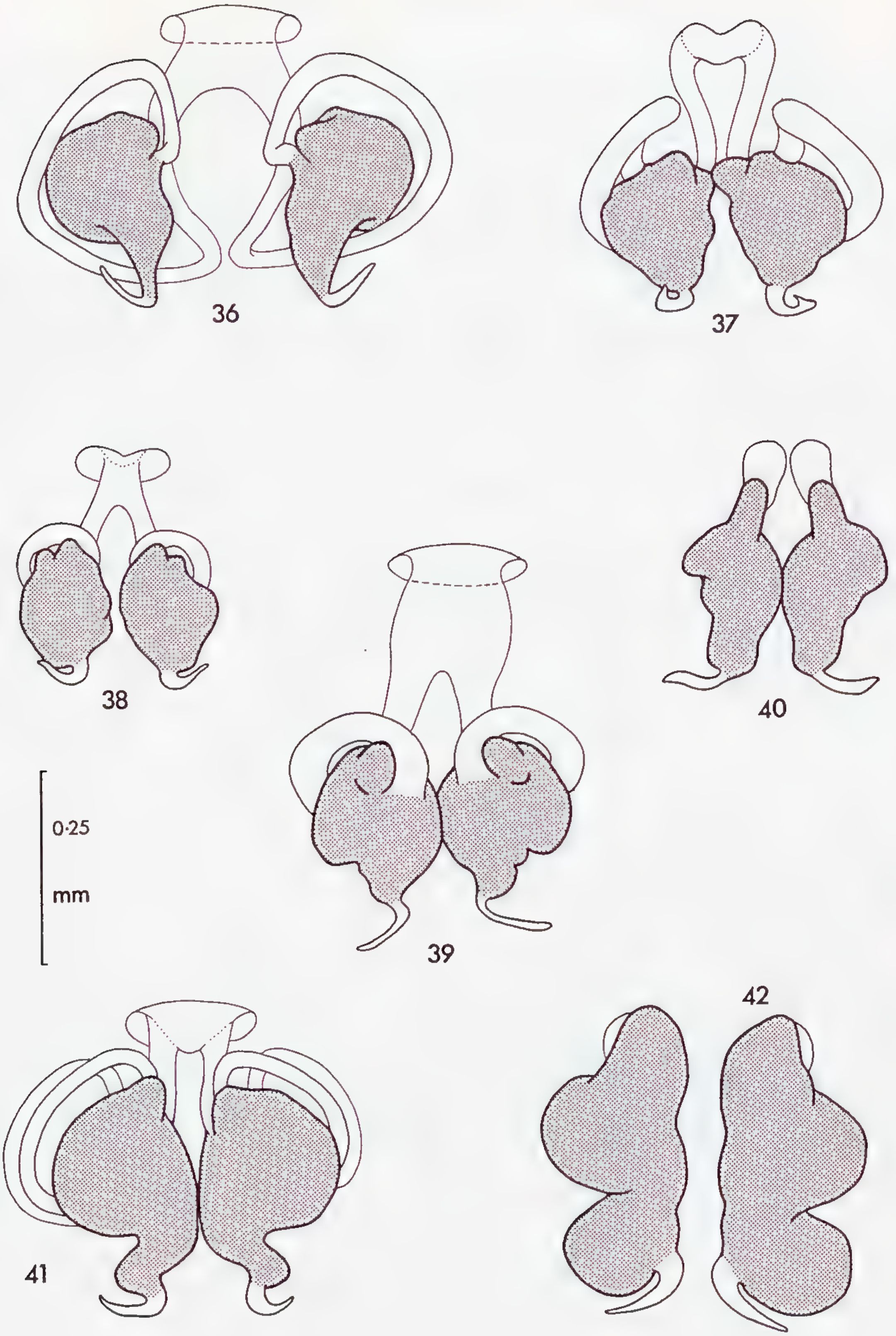
*Epimecinus tegenarioides* Simon, 1908: 378

*Baiami tegenarioides* Lehtinen, 1967: 218

*Tartarus tegenarioides* Gray, 1973: 215

FEMALE: Dimensions (mm) — Carapace length 5.75-7.36; width 3.90-5.01. Abdomen length 5.80-11.50; width 3.85-7.55. Colour — Carapace pallid grey with a large patch of dark grey pigment in front of the fovea. A broad sinuous band of dark grey pigment extends around the lateral thoracic margins. Abdomen grey overall, palest anteriorly with pigmentation in form of large, well spaced spots and darkest posteriorly with pigment spots small and more approximated. A more or less defined pale mid-dorsal anterior stripe is followed by several pale posterior chevrons. Ventral abdomen pale grey. *Eyes* — Diameters (mm): AME 0.16; ALE 0.26; PLE 0.24; PME 0.24. Interdistances (mm): AME-AME 0.16; AME-ALE 0.32; ALE-PLE 0.16; PLE-PME 0.44; PME-PME 0.44. M.O.Q. (mm): posterior width 0.92; anterior width 0.48; length 0.94. Clypeus height 4.19 diameters of an AME. Cheliceral teeth — Retromargin, 2 widely separated; Promargin, 5. *Legs* — 1423, long. Tarsi curved. Spination: LEG I, femur p1111, tibia p1111, r0111, metatarsus v220; LEG II, tibia p0111, r1111; LEG III, tibia v212; LEG IV, femur d2122, tibia v211. *Female genitalia* — Epigynum a strongly sclerotised, raised plate with a shallow median longitudinal extension into which the spermathecal ducts open on each side. Ducts short and broad. Spermathecae elongate, subdivided into two distinct bulb-like sections. Spermathecae narrowly separated.

MALE: Dimensions (mm) — Carapace length 5.65-6.12; width 4.20-4.36. Abdomen length 5.00-5.50; width 2.75-3.30. *Eyes* — Diameters (mm): AME 0.15; ALE 0.21; PLE 0.20; PME 0.21. Interdistances (mm): AME-AME 0.12; AME-ALE 0.22; ALE-PLE 0.11; PLE-PME



Figs. 36-42. Female internal genitalia, dorsal. 36, *B. loftyensis*. 37, *B. torbayensis*. 38, *B. montana*. 39, *B glenelgi*. 40, *B. brockmani*. 41, *B. volucripes*. 42, *B. tegenarioides*.

0.31; PME-PME 0.31. M.O.Q. (mm): posterior width 0.72; anterior width 0.42; length 0.76. Clypeus height. 2.87 diameters of an AME. *Legs* — Spination: LEG I, femur d22122, metatarsus p1101, v220; LEG II, femur d21122, tibia p0111, r1111; LEG III, tibia v212; LEG IV, femur d11122, tibia v211. *Male palp* — Cymbium length-width ratio 3:1. Two basal processes, a large process arising from the dorsal retrolateral aspect of the cymbial base and below this, a smaller process projecting from the retrolateral aspect. Apical part of cymbium very slender, conical, flexed dorsally and much longer than basal part. Origin of embolus basal. Embolic duct visible on tegulum. Embolus makes a half turn from origin, terminating on anterior conductor process. Terminal processes of conductor subapical on retrolateral side. Anterior process broad, spiniform (2 times as long as wide), tip directed apically; posterior process a narrow, bluntly pointed spoon. Conductor margin indented distally, anterior process set at obtuse angle to it. Tibia 5 to 6 times as long as wide and two-thirds the length of the patella. Head of tibia flexed ventrally. Retrolateral tibial process a narrow lamina with a short, thick spiniform extension, directed dorsally.

TYPES: Not available, presumed lost — Juveniles, Southwest Australia, W. Michaelsen and R. Hartmeyer, 1905. *Neotype:* KS 003 — Male, Connollys Cave, Margaret R., W.A., 17.v.1970, J. Lowry. Erection of a neotype for *Baiami tegenarioides* (Simon) is proposed on the basis of the following information — enquiries regarding the whereabouts of the original type specimens of *B. tegenarioides* have been made to the museums in which E. Simon's type specimens were lodged, namely the Museum National D'Historie Naturelle, Paris (Dr M. Hubert), The Zoologisches Museum, Humboldt Universität, Berlin (Dr M. Moritz) and the Zoologisches Institut und Zoologisches Museum, Hamburg (Dr G. Rack). Dr Moritz informed me that type specimens of *Epimecinus tegenarioides* Simon were once held in the Zoologisches Museum collections but are now presumed lost. Dr Hubert and Dr Rack indicated that the type specimens are not held in their respective collections.

RECORDS: KS 004 — Females, Easter Cave, nr. Augusta, W.A., 12.ix.1965, J. Lowry. KS 1703 — Male, Strong's Cave, nr. Augusta, W.A., 19.vi.1965, J. Lowry. KS 1704 — Female and juv., Easter Cave, W.A., 12.i.1966, J. Lowry. KS 1705 — Female and juv., Shannon R., W.A., 22.i.1973, M. Gray. KS 1706 — Female and juv., Shannon, Sutton Block, W.A., 16.xi.1971, J. A. Springett. KS 1707 — Juv., Brockman Nat. Pk., Picnic area, W.A., 22.i.1973, M. Gray. KS 1708 — Juv., Strong's Cave, nr. Augusta, W.A., 20.vi.1965, J. W. J. Lowry. KS 1709 — Juv., Calgadup, W.A., 2.i.1971, J. W. J. Lowry, KS 1710 — Juv., Golgotha Cave, nr. Wichcliffe, W.A., 24.i.1975, M. Gray. KS 3106 — Male, female and juvs., Hilltop Rd., Walpole-Nornalup Nat. Pk., W.A., Feb. 1979, M. Gray. BS 0867 (S.A. Mus. coll.) — Female, Conference Cave, Margaret R., W.A., 8.i.1965, E. Hamilton Smith. 74/1 (W.A. Mus. coll.) — Female, Bridge Cave, Margaret R., W.A., Easter 1970, A. Page. 74/16-19 (W.A. Mus. coll.) — Juv., 12 mls. W. of Manjimup, W.A., 11.iii.1971, H. Butler. 74/22 (W.A. Mus. coll.) — Juv., 3 mls. E. of Dwellingup, W.A., 24.iii.1971, H. Butler.

## BEHAVIOURAL NOTES

These spiders construct more or less horizontal sheet webs (Fig. 45, upper) of cribellate silk extending out from a retreat funnel for as much as 100cm. in *B. tegenarioides* and as little as 7cm. in *B. stirlingi*. In some of the larger webs the lower border of the retreat funnel is extended outwards for a short distance giving the impression of a second, smaller sheet below the main upper sheet. The spider moves on the under side of the sheet which is commonly guyed out into surrounding vegetation. The retreat funnel extends back into the shelter of a hole or crevice in or under the soil bank, log, stump or rock from which the sheet is slung. Species such as *B. tegenarioides*, *B. volucripes* and probably *B. glenelgi* are troglophilic and can commonly be found

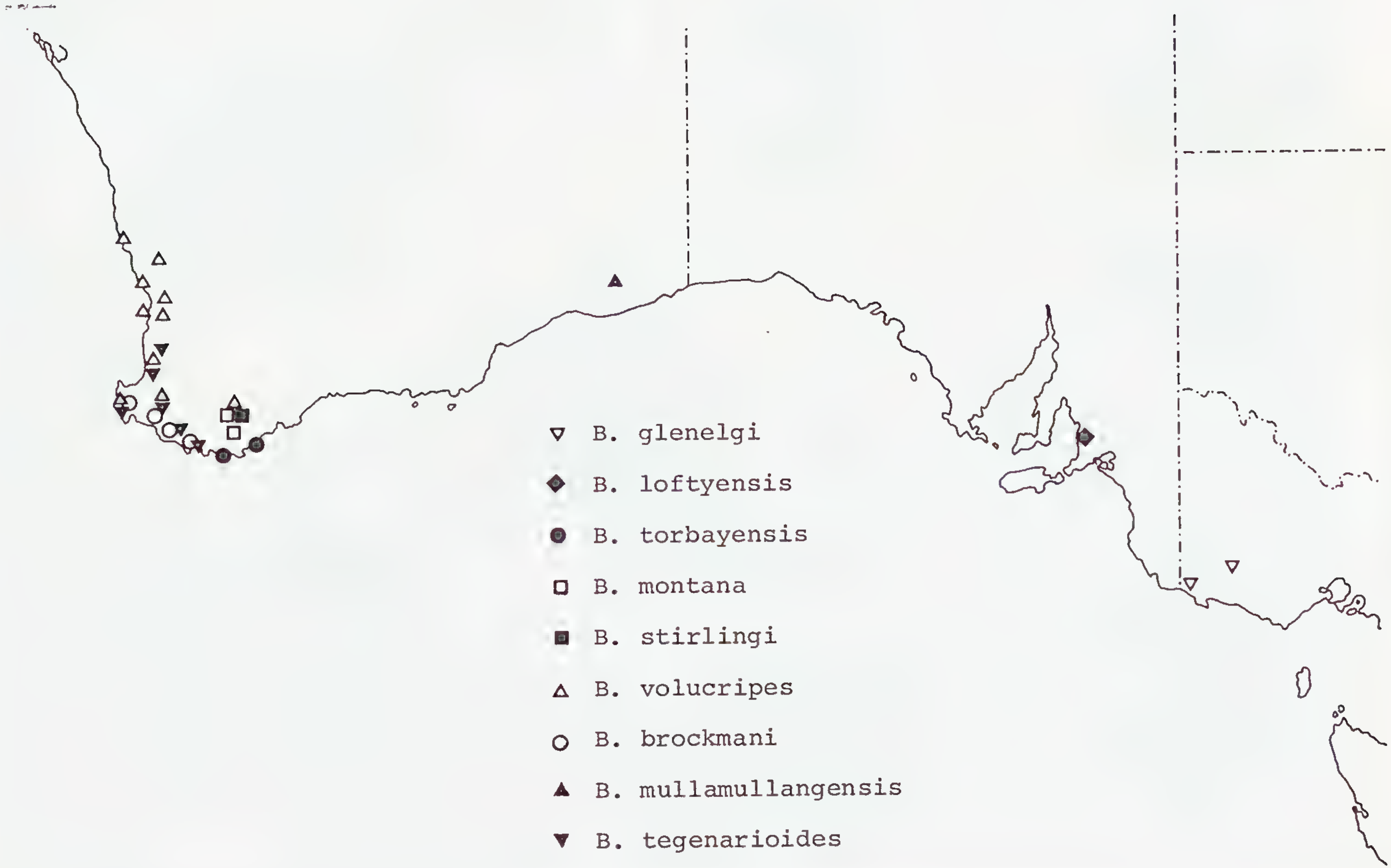


Fig. 43. Distribution of species in the genus *Baiami* from southern Australia.

occupying cave entrance and twilight zones where their webs are slung among rockpiles or between rock walls.

A significant modification of the sheet web configuration is seen in the web of the troglobitic species, *B. mullamullangensis* (Gray, 1973). This spider constructs a broad, short, funnel shaped cribellate web inside which it sits on the rock wall to which the circular base of the web is attached (Fig 45, lower). This web could be derived simply by enlargement of the retreat funnel section of the normal web, so that the funnel now serves both retreat and catching functions and the horizontal sheet component is eliminated. The hypochilid spider, *Hypochilus gertschi,* constructs a very similar type of web on rock walls in cave-like habitats (Shear, 1967).

The egg sacs form slightly irregular spheres constructed of a closely woven inner and loose outer layers of silk onto which particles of soil and litter are attached. The sac, containing nonglutinous eggs, is suspended within the retreat funnel. At least two egg-sacs may be made during the summer-autumn breeding period. *Baiami* females do not construct a closed brood chamber for the sacs although an irregular barrier network of threads may be erected in the retreat funnel.

Mated females, particularly in the *tegenarioides* group, may have their epigynal structure obscured by a hard plug which presumably functions to prevent subsequent matings.

## PHYLOGENY AND DISTRIBUTION

A preliminary scheme of relationships based on sexual characters (Table 1) is given in the form of a cladogram (Fig. 44). Two species groups are recognised: the *glenelgi* group *(B. glenelgi, B. loftyensis, B. torbayensis, B. volucripes, B. stirlingi, B. montana)*, characterised by the apomorphic possession of a deeply invaginated epigynal fossa; and the *tegenarioides* group *(B. brockmani, B. tegenarioides, B. mullamullangensis)* characterised by the apomorphic possession of a basal origin of the embolus, uncoiled spermathecal ducts and an apical ventral flexure of the tibia. *B. stirlingi* has affinities with *B. montana* but its final placement will have to wait until female specimens are available.

The generic relationships of *Baiami* remain uncertain. Lehtinen's (1967) placement of the genus in his Amaurobiidae: Stiphidiinae was based partly on New Caledonian material now excluded from *Baiami*. Possible relationship with the Tasmanian genus *Tjurunga* Lehtinen 1967 will be clarified only with the collection of additional material, especially males. Forster (1973) places *Baiami* (syn. *Tartarus*) within his Stiphidiidae with what seems to be a somewhat diverse assemblage of genera, the inclusion of *Corasoides* and *Stiphidion* being particularly questionable. However, the closest relatives of *Baiami* include several undescribed genera from S.E. Australia. One of these is of particular interest because it possesses a large median apophysis which, in position and shape, closely corresponds to the posterior conductor process present in *Baiami*. If this relationship is correct it suggests that this process may represent a fused median apophysis in *Baiami* rather than a true conductor element.

The distribution of *Baiami* (Fig. 43), as now constituted, is confined primarily within the southern Australian humid-subhumid climatic zones west of the Grampian Range in association with forest, riparian and karst habitats. The one exception is the cavernicolous relict species *B. mullamullangensis* from a southern arid zone karst. Species richness is greatest in the southwest where seven species occur, including representatives of both species groups. The two south-eastern species both belong to the *glenelgi* group.

TABLE 1. Proposed character states for the genus *Baiami*.

| | PLESIOMORPHIC STATE | APOMORPHIC STATE |
|---|---|---|
| CYMBIUM | | |
| 1. Basal processes | absent | present |
| 2. Number of basal processes | 1 | 2 |
| 3. Dorsal flexure | present | absent |
| 4. Apical shape | coniform | digitiform |
| EMBOLUS | | |
| 5. Embolic coil | single | double |
| 6. Origin | apical-lateral | basal |
| CONDUCTOR | | |
| 7. Anterior process shape | triangular | attenuate |
| 8. Anterior margin | gently curved | straight |
| TIBIA | | |
| 9. Retrolateral spine slope | apical | dorsal |
| EPIGYNUM | | |
| 10. Fossa | absent | present |
| 11. Posterior margin of fossa | weakly sclerotised | strongly sclerotised |
| 12. Posterior margin width | narrow | broad |
| 13. Shape of fossa opening | broad, oval | small, subcircular |
| INTERNAL GENITALIA | | |
| 14. Coiling of ducts | loose | tight |
| 15. Spermathecal duct openings | not visible externally | visible externally |

*Baiami* seems to have had a long history in southern Australia. Perhaps as early as the middle Miocene, when warm temperate-subtropical climates prevailed across southern Australia, representatives of both the *glenelgi* and *tegenarioides* groups were already in existence; the former ranging right across southern Australia to the western margin of the marine Murray Basin, while the latter were more south-western in their distribution (in any event, the *tegenarioides* group has left no known eastern representatives). With the onset of drier conditions in the later Miocene-Pliocene trans-southern distributions were disrupted and contracted into eastern and western refuge areas where relatively moist climatic conditions still prevailed. An early consequence of this progressive environmental drying may have been the origin of *B. volucripes* which is both the most widely distributed and apparently environmentally tolerant of the western species of *Baiami*. The remaining western species were restricted to moist areas associated with forest habitats on the southern coastal and highland regions, such as the Porongorup and Stirling Ranges. Johnstone et al. (1973) suggest that these ranges may have a long tertiary history extending back to Eocene times.

Subsequent speciation within the genus seems related to continuing climatic and eustatic fluctuations associated with Pliocene and Pleistocene glaciation. The origin of the species *B. brockmani*, *B. montana* and *B. stirlingi* may be attributed simply to episodes of fragmentation of the south western forest region into isolated southern coastal and highland areas during 'interpluvial' phases. West to east trans-southern range extensions may have been involved in the origin of some species, notably the sister species pairs *B. torbayensis* – *B. loftyensis* and *B. tegenarioides* – *B. mullamullangensis*. Such E↔W 'migrations' presumably became possible under 'pluvial' climatic regimes,

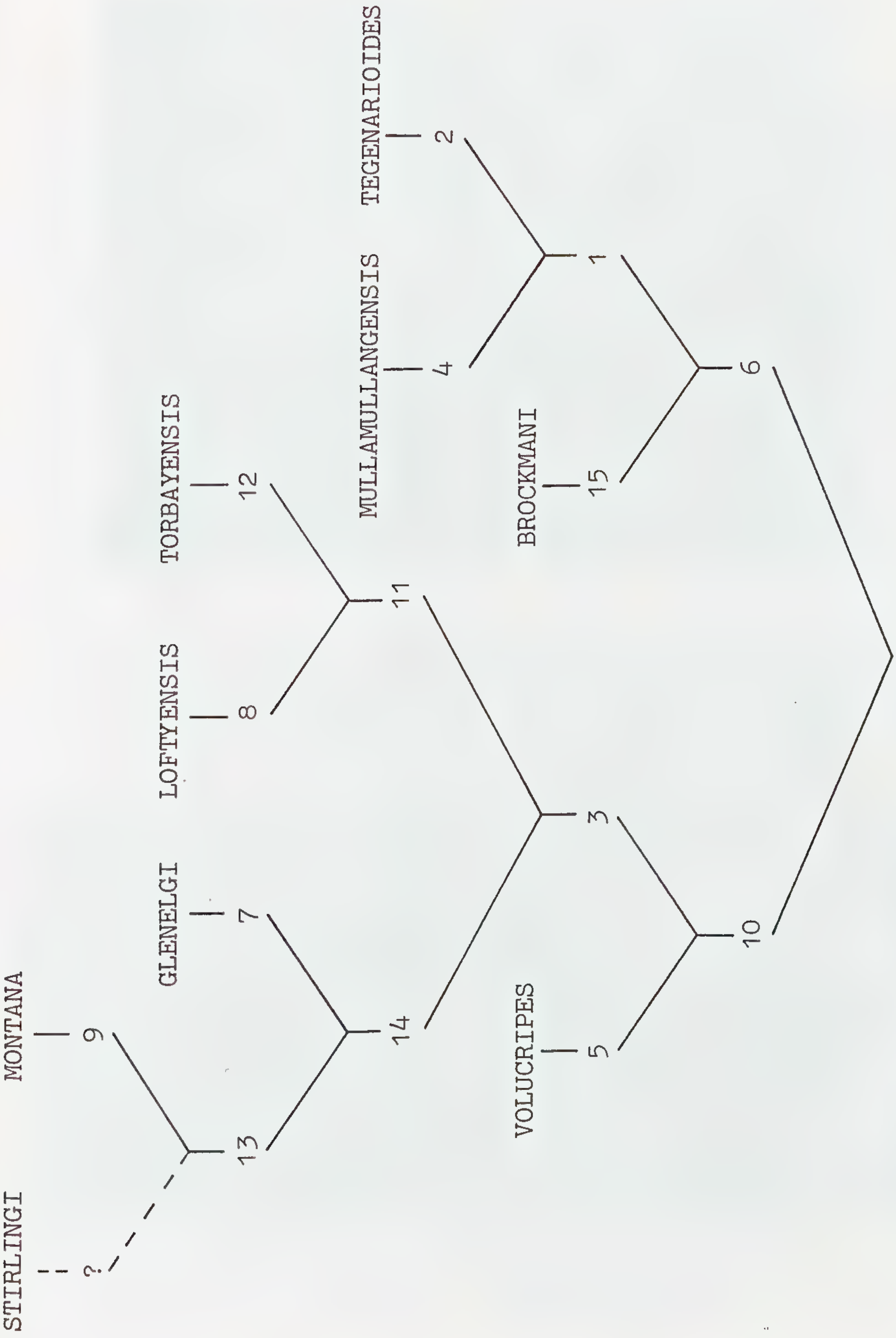


Fig. 44. Cladogram of relationships within the genus *Baiami*.

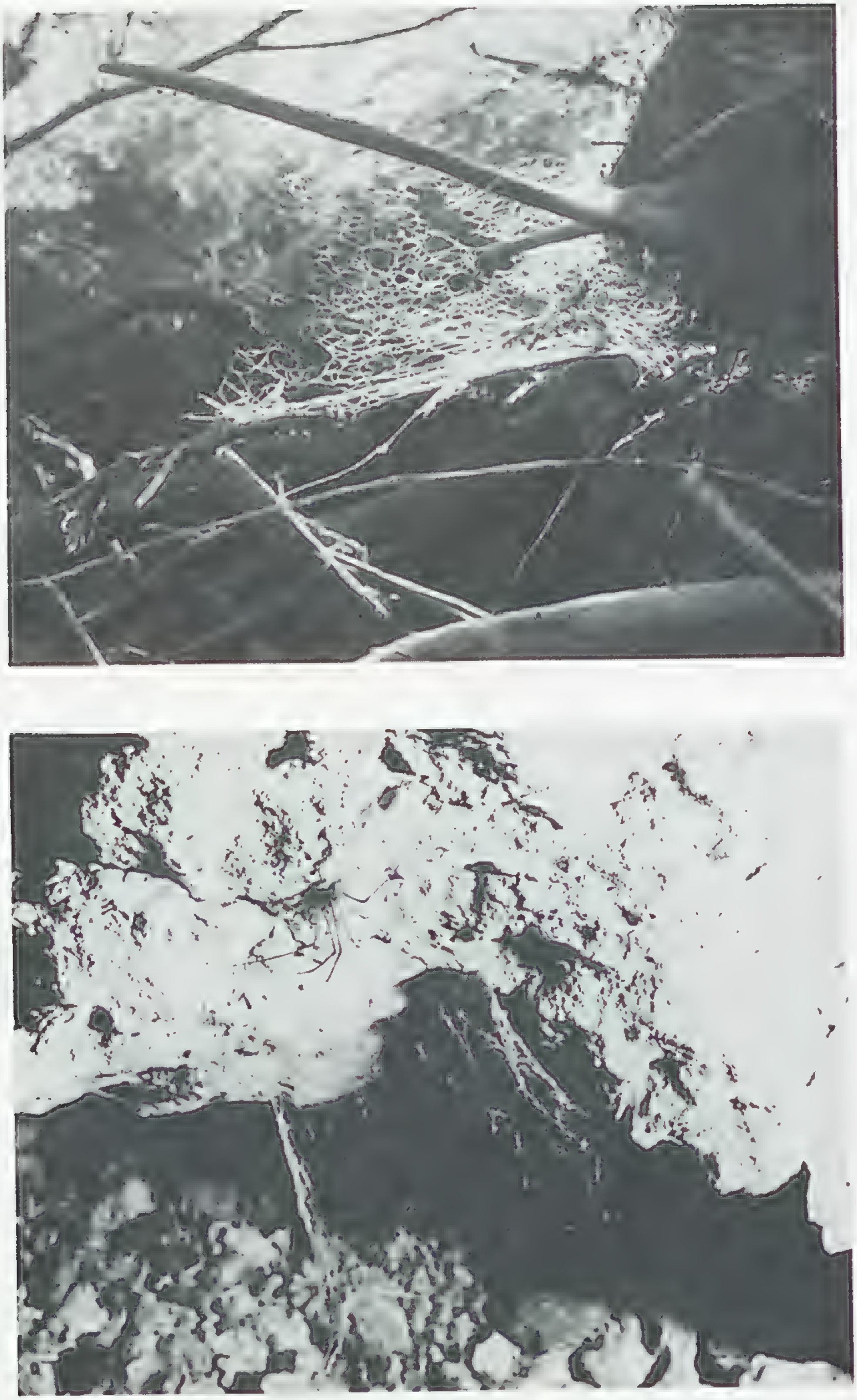


Fig. 45. Upper: *B. tegenarioides,* sheet web on soil bank. Lower: *B. mullamullangensis,* spider in web on cave rockpile.

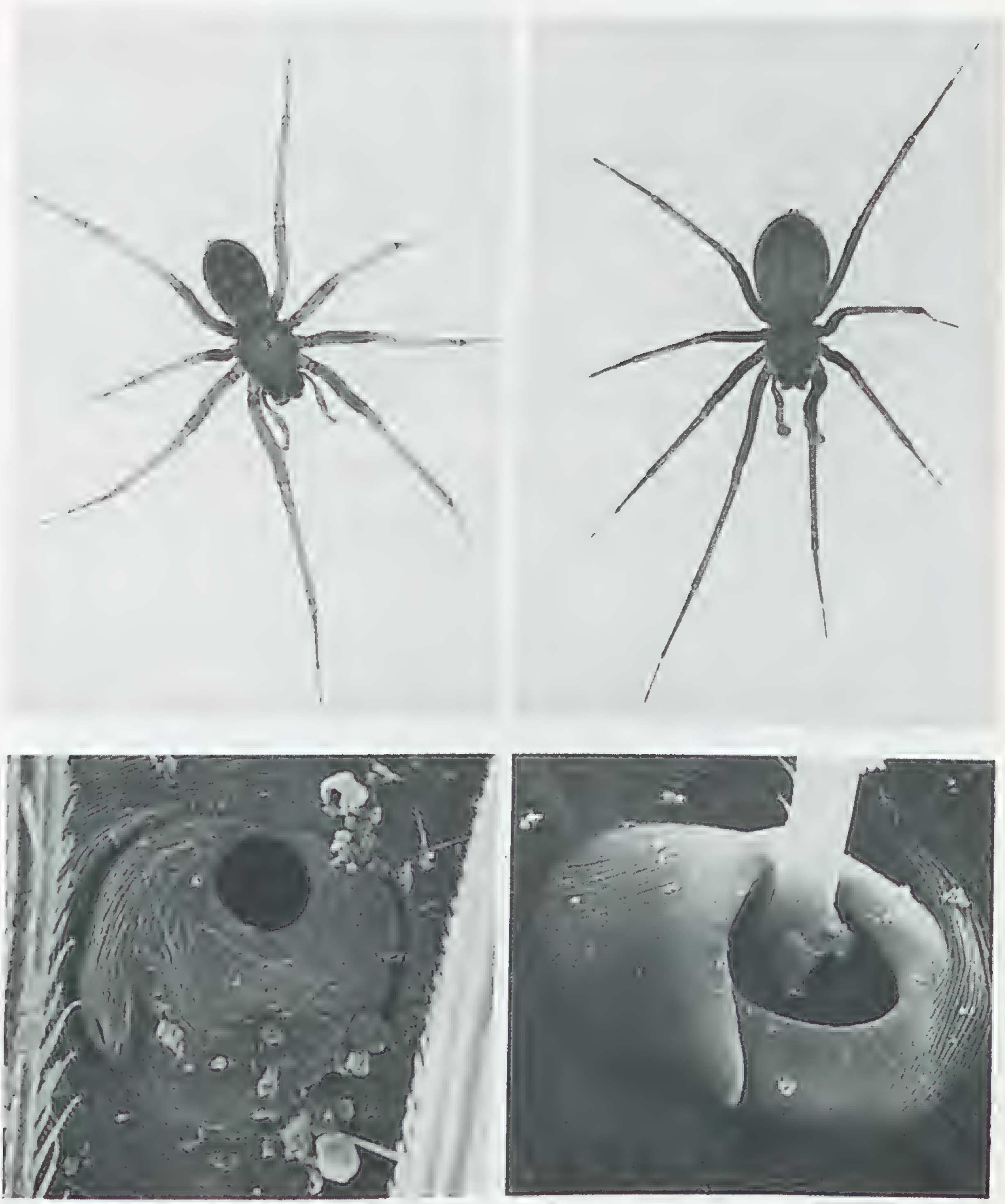


Fig. 46. Upper left: *B. volucripes,* dorsal. Upper right: *B. brockmani, dorsal.* Lower left: *B. mullamullangensis,* tarsal organ (x 1040). Lower right: *B. tegenarioides,* trichobothrium base, metatarsus (x 780).

speciation occurring with population isolation during subsequent 'interpluvials'. Examples of this have been given for several animal groups, notably frogs (Main, 1970). A considerably more speculative speciation event involving an early E↔W range extension relates to the suggested origin of *B. glenelgi* in the east and the progenitor speices of *B. montana* and *B. stirlingi* in the west, if indeed the latter prove to be sister species as tentatively postulated here.

## ACKNOWLEDGEMENTS

My thanks to Dr B. Y. Main who made available material from her personal collection. Dr M. Moritz and Dr M. Hubert kindly loaned type material from the collections of the Natural Museum, Paris and the Zoological Museum, Berlin respectively. Inking and shading of drawings was done by Ms P. Greer.

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Manuscript accepted for publication 27 March, 1980

# PLEISTOCENE ZIPHODONT CROCODILIANS OF QUEENSLAND

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## SUMMARY

The rostral portion of a crocodilian skull, from the Pleistocene cave deposits of Tea Tree Cave, near Chillagoe, north Queensland, is described as the type of the new genus and species, *Quinkana fortirostrum*. The form of the alveoli suggests that a ziphodont dentition was present. A second specimen, referred to *Quinkana* sp. from the Pleistocene cave deposits of Texas Caves, south Queensland, confirms the presence of ziphodont teeth. Isolated ziphodont teeth have also been found in eastern Queensland from central Cape York Peninsula in the north to Toowoomba in the south. *Quinkana fortirostrum* is a eusuchian, probably related to *Pristichampsus*. The environments of deposition of the beds yielding ziphodont crocodilians do not provide any evidence for (or against) a fully terrestrial habitat for these creatures. The somewhat problematic Chinese *Hsisosuchus chungkingensis* shows three apomorphic sebecosuchian character states, and is thus considered a sebecosuchian.

## INTRODUCTION

The term ziphodont crocodilian refers to those crocodilians possessing a particular adaptation in which a relatively deep, steep sided snout is combined with laterally flattened, serrate teeth (Langston, 1975). Although such crocodiles were described in the nineteenth century (Cuvier, 1824; Marsh, 1871) little attention was paid them until Colbert (1946) redescribed *Sebecus icaeorhinus* from Argentina. The nearly contemporaneous description of *Baurusuchus pachecoi* (Price, 1945) in which the ziphodont condition reaches its most extreme expression, also attracted interest toward these forms. Langston (1956) demonstrated that there were two phylogenetically distant forms of ziphodont crocodile, the mesosuchian sebecoids and the eusuchian pristichampsines. Although Colbert (1946) had proposed that sebecosuchians deserved subordinal status, this was not widely accepted until the study of Gasparini (1972).

Sebecosuchians appear first in the Chinese Jurassic (Young and Chow, 1953; Langston, 1956), and are most numerous in South America, ranging from the Upper Cretaceous to the Miocene (Molnar, 1978), although two reportedly sebecosuchian genera derive from the Eocene of Europe (Berg, 1966; Antunes, 1975). Pristichampsines first appear in the Paleocene of China (Li, 1976) and are widely distributed through Europe and North America in the Tertiary (Langston, 1975; Steel, 1973). They became extinct in the northern continents with the end of the Eocene (Molnar, 1978), but may have survived in Africa into the Miocene (Andrews, 1914).

Prior to 1970, only isolated ziphodont teeth had been reported from Australasia, from two localities of the Otibanda Formation in New Guinea (Plane, 1967). During exploration of Tea Tree Cave near Chillagoe, north Queensland, in 1970 Lyndsey Hawkins, of the Sydney Speleological Society, discovered the snout of a ziphodont crocodilian. In 1975 Michael Archer discovered a second ziphodont crocodilian in the deposits at The Joint, one of the Texas Caves in southern Queensland. Soon afterwards ziphodont teeth and fragments were recognised from several other Australian localities, all but one in Queensland. The single South Australian ziphodont crocodilian, from the Pliocene of Lake Palankarinna (Hecht and Archer, 1977) is not treated here.

Records of The Australian Museum, 1981, **Vol 33 No. 19,** 803-834, Figures 1-14

The discovery of ziphodont crocodilians in Australia, is of interest zoogeographically (cf. Molnar, 1977) and stratigraphically. While ziphodont crocodilians elsewhere became extinct at the end of the Miocene, the Australian forms survived well into the Pleistocene (Molnar, 1978; Hecht and Archer, 1977).

COLLECTION DESIGNATIONS:

AM — Australian Museum, Sydney
FMNH — Field Museum of Natural History, Chicago
ME — Museum für Erdgeschichte-Geiseltalsammlung, Halle
QM — Queensland Museum, Brisbane
UCMP — Museum of Paleontology, University of California, Berkeley
YPM — Peabody Museum of Natural History, Yale University, New Haven

Order CROCODILIA

Suborder EUSUCHIA Huxley, 1875

Family CROCODYLIDAE Cuvier, 1807

Genus **Quinkana,** nov.

Species **Quinkana fortirostrum,** nov.

ETYMOLOGY: The generic name is from *Quinkan,* a term, probably from the Gugu-Yalanji tribe, denoting a spirit (Trezise, 1971). Quinkans are associated with crocodiles in at least one of the rock art sites in southeastern Cape York. This name is given neuter gender. The specific name is from Latin, *fortis,* strong, and *rostrum,* beak, here used in the sense of snout.

TYPE SPECIMEN: Australian Museum F.57844: a cranial rostrum lacking anterior end and teeth.

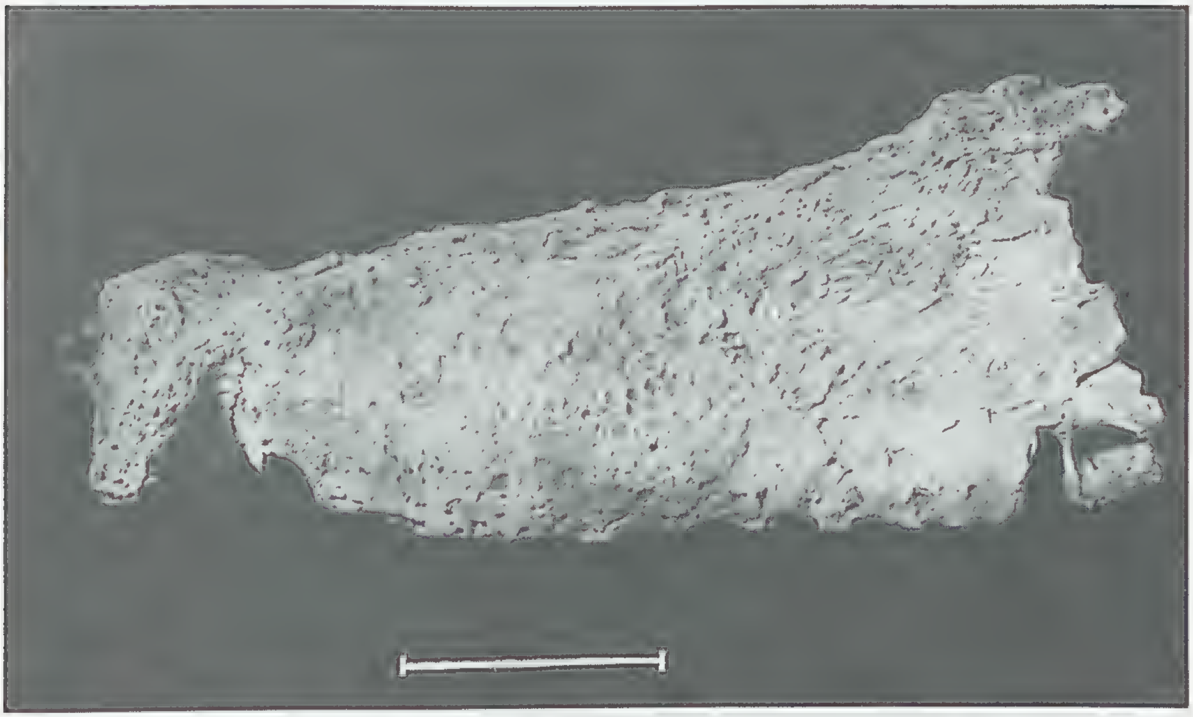
LOCALITY: Tea Tree Cave, near Chillagoe, north Queensland.

AGE: Pleistocene (Molnar, 1978).

DESCRIPTION OF TYPE SPECIMEN: The illustrations (Fig. 1, 2, 3, 4) show the features of the type specimen of *Quinkana fortirostrum.* A brief description has already appeared (Molnar, 1977), hence this description will emphasize those features important for taxonomic analysis or not previously noted.

*Premaxilla:* Both premaxillae are present, with the right almost complete. A raised rim surrounds the confluent external nares. Extending posteriorly from the dorsal body of the premaxilla, a short posterior process separates the anterior portion of the nasal from the anterior portion of the maxilla. On the palate, the maxillary-premaxillary junction is U-shaped with the convexity directed posteriorly. That portion preserved of the incisive foramen suggests that this foramen was broader transversely than long. From the incisive foramen a shallow trough extends posteriorly across the premaxillae and into the maxillae.

Four alveoli are present in the right premaxilla, in an alveolar process. The posterior two are elongate in form, while the third from the back is more nearly circular. A deep pit,



1. *Quinkana fortirostrum*, AM F.57844. Snout in lateral aspect. Scale 5 cm. Note that portions of three alveoli can be seen at the lower right.

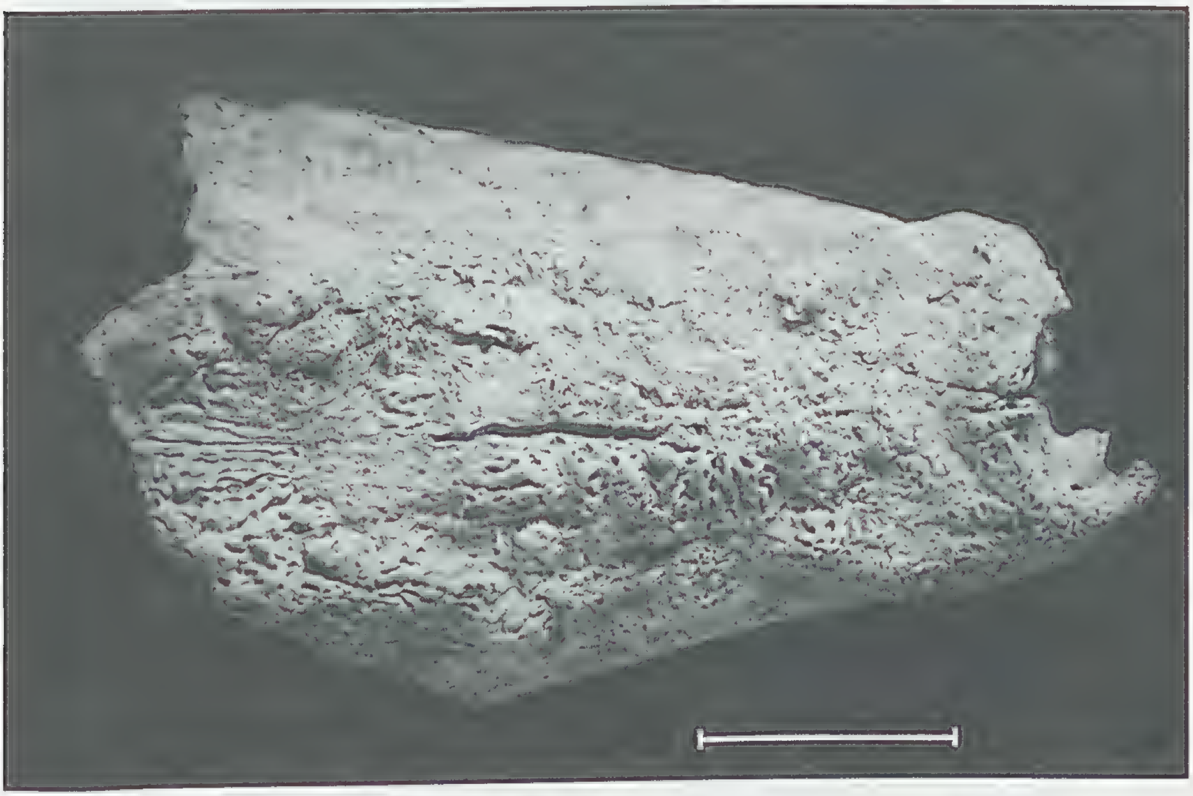


Fig. 2. *Quinkana fortirostrum*, AM F.57844. Snout in dorsal aspect. Scale 5 cm.

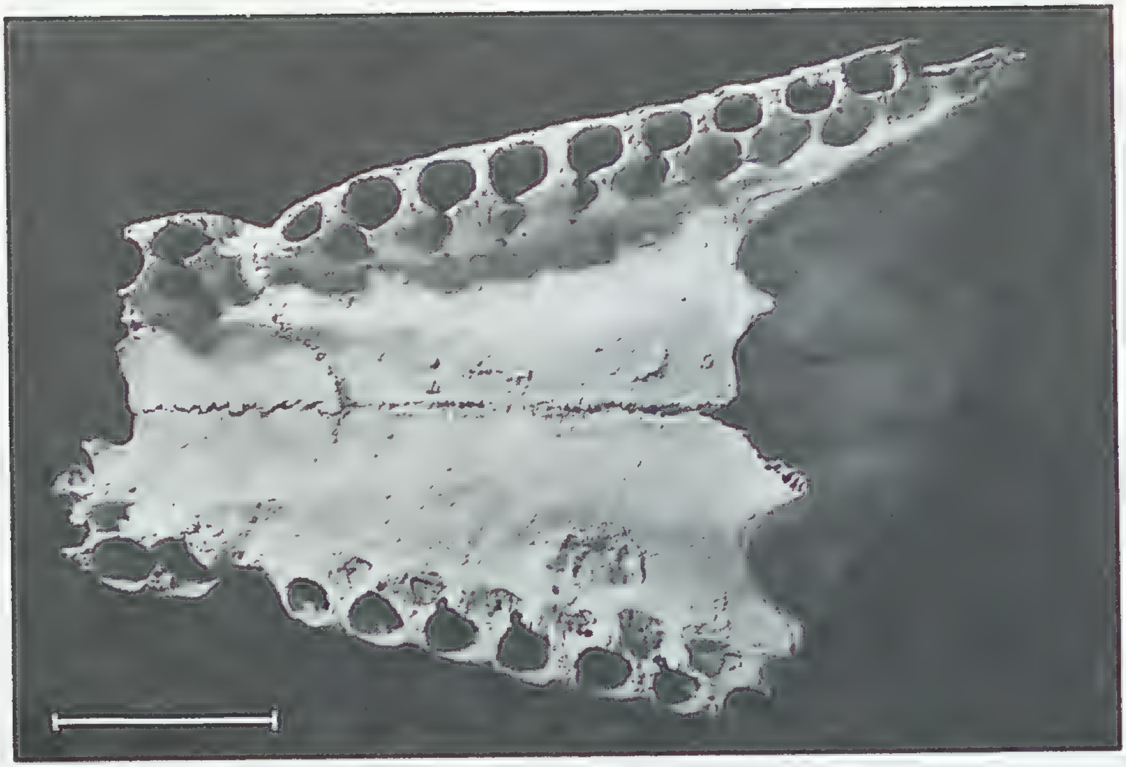


Fig. 3. *Quinkana fortirostrum*, AM F.57844. Snout in ventral aspect. Scale 5 cm.

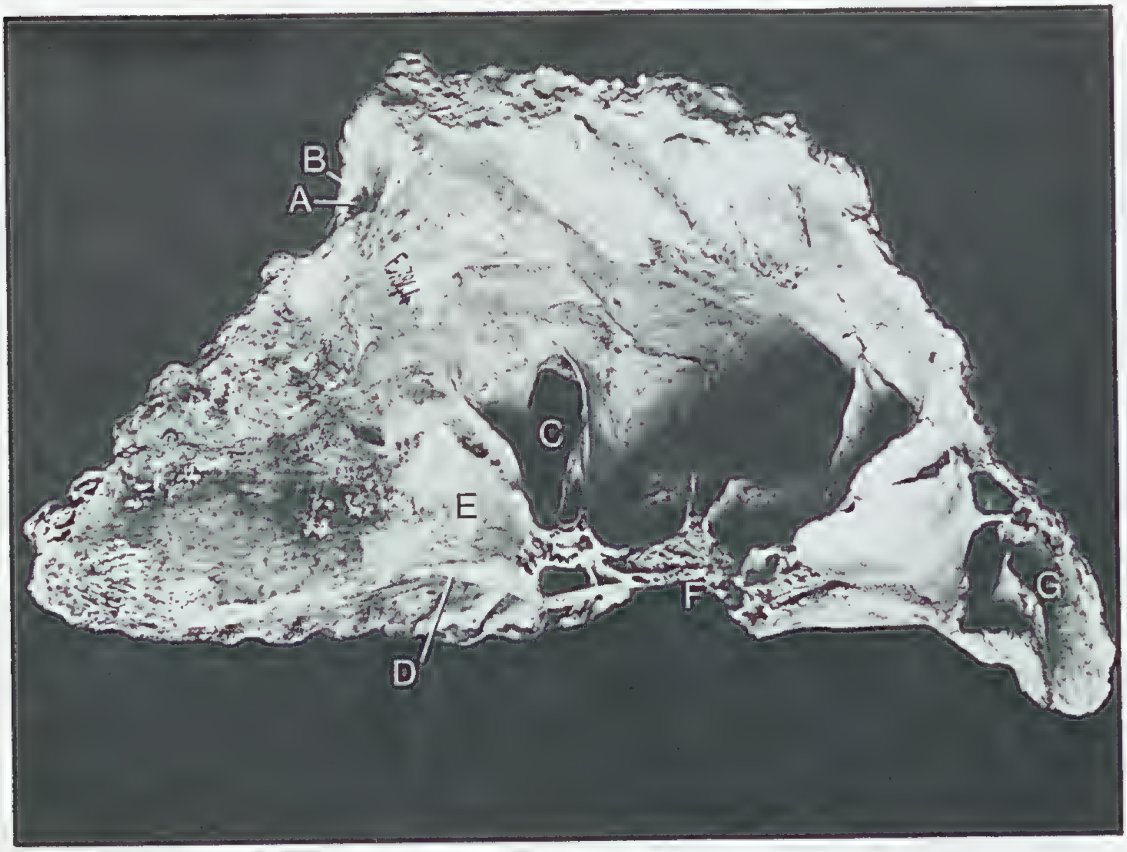


Fig. 4. *Quinkana fortirostrum*, AM F.57844. Right oblique posterior view, into nasal cavity. **A.** nasolachrymal canal, **B.** orbital margin, **C.** lateral chamber, **D.** anterior margin of palatal fenestra, **E.** anterior rim of palatal fenestra, **F.** palate, **G.** alveolus in section.

lacking the posterior wall of an alveolus, lies between the remnant of the anteriormost alveolus preserved and the incisive foramen (Fig. 3). Fossae for the reception of dentary teeth lie just medial to the alveolar process.

*Nasal:* Both nasals are complete, but have separated slightly along the midline. Their sides are parallel, tapering markedly anteriorly and slightly posteriorly. The nasals separate the two premaxillae anteriorly and project as a posterior nasal spine into the external nares. The corresponding portion of the premaxilla is not preserved, hence it cannot be determined if an internarial bridge was present.

The nasals are but slightly arched in the coronal plane, and lie wholly on the dorsum of the snout, unlike those of sebecosuchians which form a median crest (Colbert, 1946). They are heavily sculptured.

*Maxilla:* The left maxilla is nearly complete, while the right lacks the posterolateral portion. The lateral wall of the maxilla inclines upward at an angle of from 45 degrees (posteriorly) to 60 degrees (anteriorly) to the horizontal, and is lightly sculptured. A distinct, blunt ridge crowns the anterior portion of the maxilla above the first alveolus.

The suborbital portion of the maxilla shows that the jugal did not extend in front of the anterior margin of the orbit. This condition is uncommon among crocodiles. The suborbital portion of the maxilla is of such depth as to suggest that the infraorbital bar was markedly deeper than usual among crocodilians. Although little of the palatines is preserved much of the maxillary contact for these elements is present. This indicates that the anterior process of the palatine, usually found in crocodilians, was absent from *Q. fortirostrum*. The ventral margin of the maxilla is weakly convex, without any sign of the festooning typical of most crocodilians.

A high, posteriorly concave partition dorsally bounds the anterior margin of the palatal fenestra. A similar, but less well developed partition is found in *Crocodylus johnstoni, C. novae-guineae* and *C. porosus,* where, however, it is placed well anterior to the margin of the fenestra, and is restricted to the lateral portion of the snout cavity. In *Q. fortirostrum* the maxilla is excavated anterior to this partition, forming lateral chambers that open posteriorly. Above the junction of the palatal processes of the two maxillae rise two thin, nearly vertical flanges, which together form a narrow trough along the floor of the snout cavity (Fig. 4).

Nine complete and three incomplete alveoli are found in the alveolar process of the left maxilla (the three incomplete alveoli can be seen in Fig. 1). The alveoli are elongate and subequal in size (Fig. 5). The elongate shape of the alveoli suggests that the teeth were laterally compressed (Molnar, 1977). The long axes of the alveoli parallel one another but are inclined both to the long axis of the snout and to the margin of the snout, giving the alveolar row a distinctive appearance (Fig. 3). Medially the alveolar process bears fossae for the reception of the dentary teeth. These indicate that the dentary teeth closed medial to the upper teeth, unlike the situation in the Crocodylinae where the teeth interlock.

*Frontal:* Only the anterior extremities of the frontals remain. They are heavily sculptured, and extend two cm further anterior on the ventral than on the dorsal surface.

*Prefrontal:* The anteriormost portions of both prefrontals are present. They are narrow, heavily sculptured, and bear a distinct knob above the anterior extremity of the orbit.

*Lachrymal:* Almost the entire left, and a portion of the right lachrymal are preserved. The lachrymal, lying on the lateral wall of the snout, makes an angle of about 45 degrees

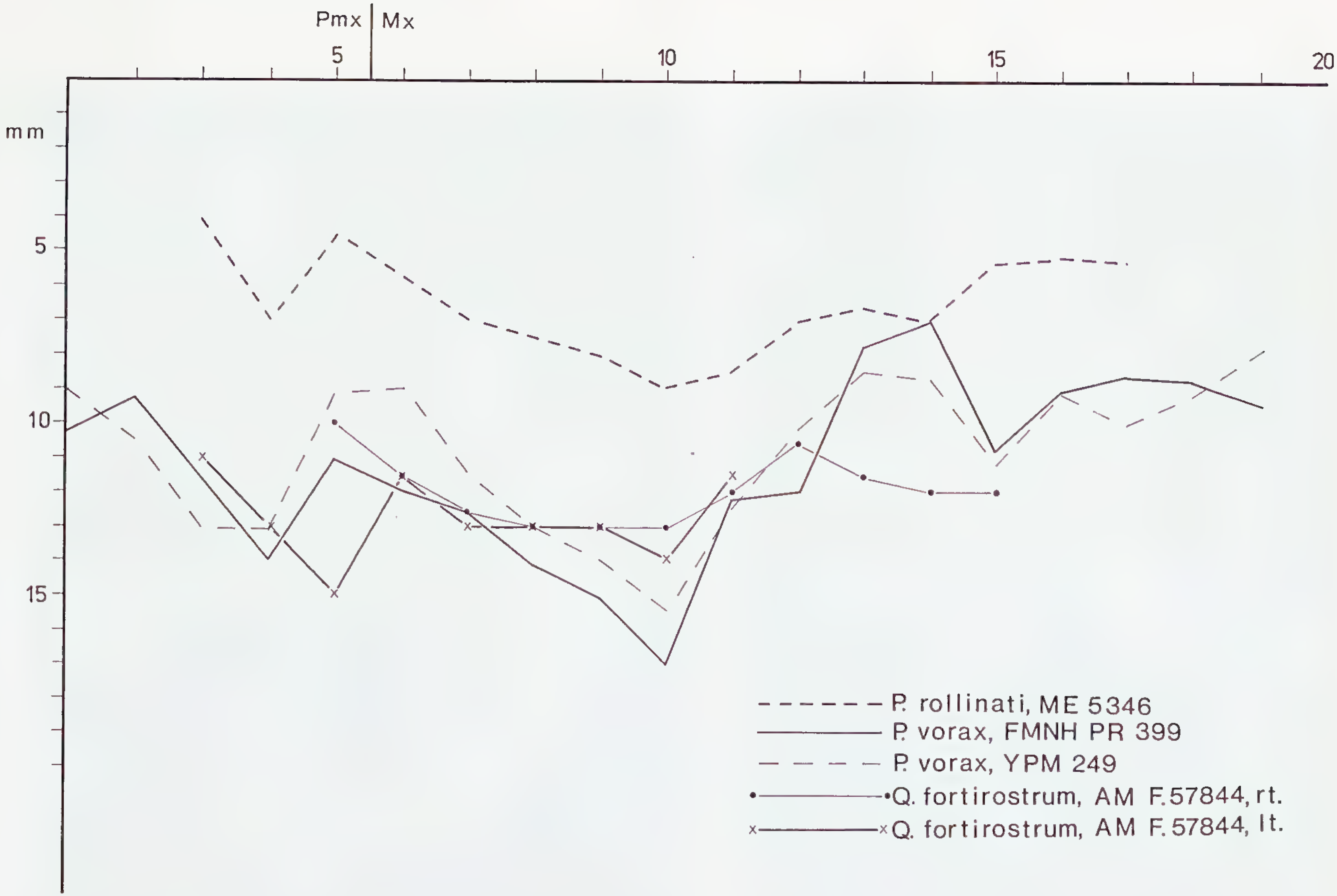


Fig. 5. Alveolar size (anteroposterior diameters) of *Quinkana fortirostrum* (AM F. 57844) compared with *Pristichampsus rollinati* (ME 5346) and *P. vorax* (FMNH PR 399 and YPM 249). (**A, B,** and **C** after Langston, 1975.)

with the prefrontal, which lies on the roof of the snout. The orbital margin of the lachrymal shows that the orbit faced laterally. Opening into the anterior margin of the orbit is the nasolachrymal canal, which is continued posteriorly along the dorsal margin of the orbit as a broad sulcus. The canal opens anteriorly on the medial surface of the lachrymal about one-third of its length back from the anterior margin.

The lachrymal exhibits two knobs along its dorsal edge, the first just anterolateral to the prefrontal knob, and the second 1.5 cm directly in front of the prefrontal knob. Although lachrymal ridges are present in some crocodilians, none known to me show knobs like those of *Quinkana*.

*Palatine:* Two small pieces of palatine are present on the dorsal surface of the palatal process of the maxilla.

*Snout form:* The snout proportions of *Q. fortirostrum,* together with those of selected comparable taxa (cf. Molnar, 1977) are given in Table 1. The snout of *Quinkana* is broader than that of *Pristichampsus,* and the sebecosuchians, and deeper than in the Crocodylinae and Alligatorinae: in the terminology proposed in the character analysis of this paper, *Quinkana* can be described as having a broad, moderately deep snout. No other crocodilians show this combination of character states.

TABLE 1. Snout proportions of *Quinkana* and comparable crocodilians.

| Taxon | H/L | H/W | W/L |
|---|---|---|---|
| *Sebecus icaeorhinus* | 0.39 | 1.37 | 0.28 |
| *Pristichampsus vorax* | 0.24 | 0.51 | 0.48 |
| *Quinkana fortirostrum* | 0.36 | 0.51 | 0.70 |
| *Osteolaemus tetraspis tetraspis* | 0.35 | 0.35 | 1.00 |
| *Osteolaemus tetraspis osborni* | 0.31 | 0.41 | 0.74 |
| *Paleosuchus palpebrosus* | 0.29 | 0.48 | 0.60 |

L is the distance from the anterior extremity of the orbit to the posterior extremity of the external nares, H is the maximum depth of the snout at the fifth maxillary alveolus, and W is the maximum breadth of the snout at the fifth maxillary alveolus. Values for the taxa other than *Quinkana* are taken from published illustrations, *Sebecus* from Colbert (1946), *Pristichampsus* from Langston (1975), and the modern taxa from Wermuth and Mertens (1961).

DEFINITION: Snout broad and moderately deep; alveoli elongate and arranged in a distinctive pattern; maxillary alveoli subequal in size; distinct alveolar process; palatal portion of maxillary-premaxillary suture U-shaped with convexity directed posteriorly; anterior process of palatine very short or absent in ventral aspect; rim superiorly adjacent to anterior margin of palatal fenestra; no portion of jugal extending anterior to the orbit; three knobs present on lachrymal and prefrontal dorsal to the anterior margin of the orbit. Because *Quinkana* is a monotypic genus, no distinction can be made between the generic and the specific diagnosis. The referred specimen (QM F.7898) suggests that ziphodont teeth were present.

THE TEXAS CAVES CROCODILE (QM F.7898): A second Pleistocene ziphodont crocodile, found at The Joint, a cave near Texas, southeast Queensland, was described by Hecht and Archer (1977). The specimen was found in a typical late Pleistocene vertebrate assemblage (Archer, 1978), in intimate association with mammalian remains: the right

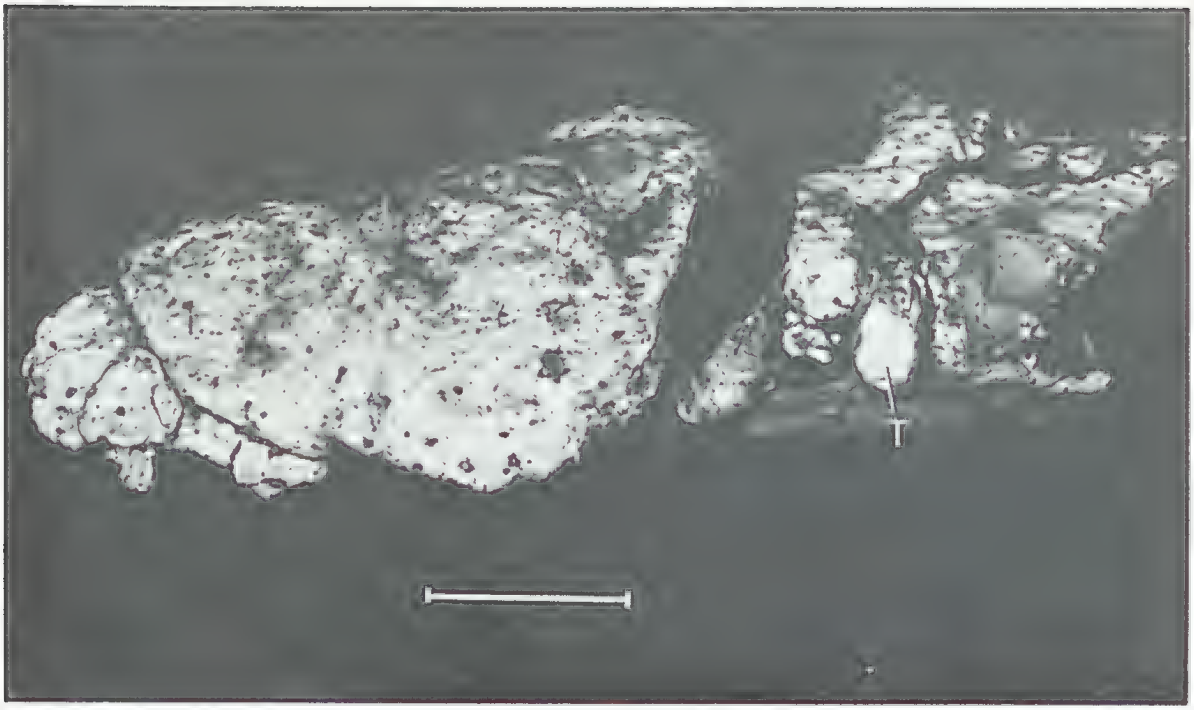


Fig. 6. *Quinkana* sp., QM F7898. Snout in lateral aspect. Scale 1 cm. **T**, ziphodont tooth *in situ*.

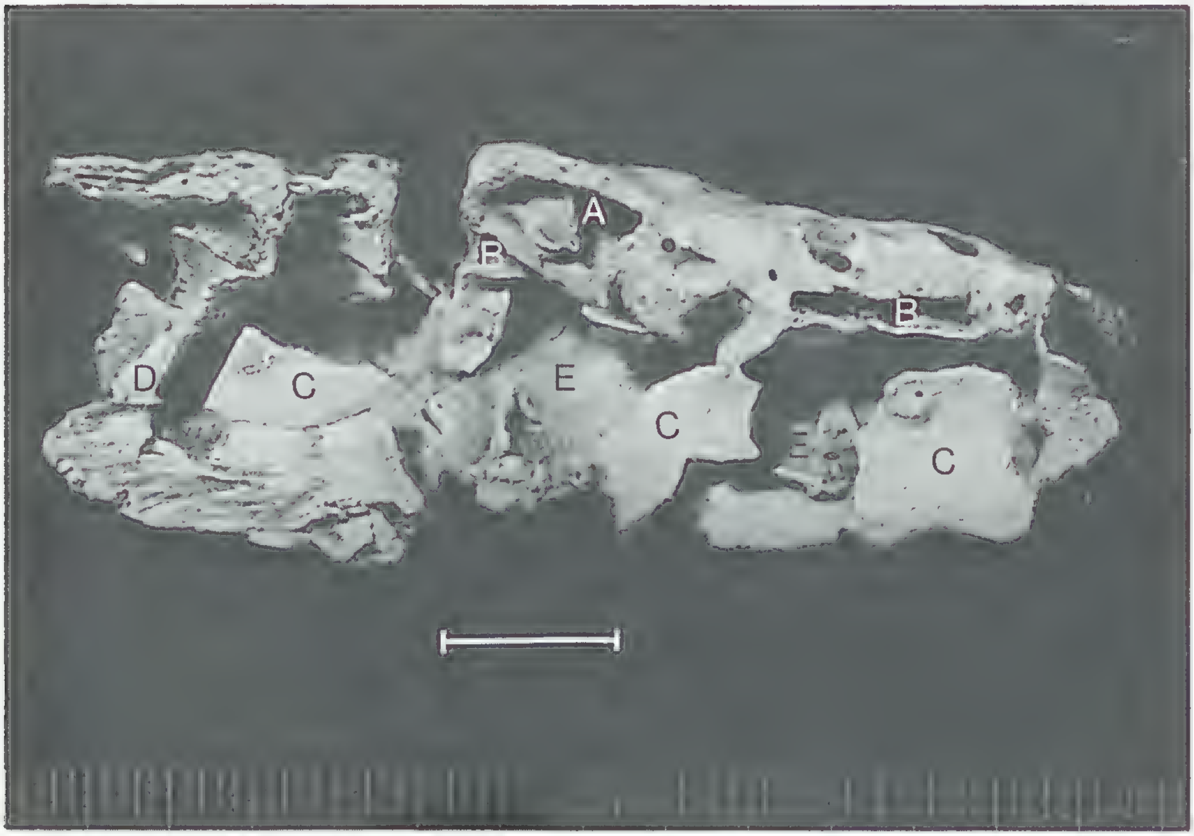


Fig. 7. *Quinkana* sp., QM F7898. Snout in medial aspect. Scale 1 cm. **A.** niche dorsal to alveolar part of maxillary wall, **B**, narrow chamber between niche and alveolar part of wall, **C.** remnants of partition dividing nasal cavity from lateral chamber, **D.** anterior rim of palatal fenestra, **E.** alveolar process.

upper molar of a small macropodine was found within the snout.

The specimen consists of the greater portion of a left maxilla, and two smaller fragments, one a flake of bone with the crown of a tooth adherent.

The palatal portion of the left maxilla is nearly complete, the lateral is less complete, with some portions of the internal partitions present (Fig. 6). The lateral wall makes an angle with the palate of 60 degrees, and appears relatively thinner and more lightly sculptured than that of AM F.57844. Six elongate alveoli are present in the same distinctive pattern as in AM F.57844.

The delicate internal partitions preserved indicate that the lateral maxillary wall was separated from the nasal cavity by an elongate chamber (4 in Fig.9) extending almost the length of the maxilla. The alveoli extend almost to the dorsal margin of the maxilla anteriorly (for the first two present), but are surmounted by a niche (1 in Fig. 9) posteriorly. A second, narrow chamber (2 in Fig. 9) extends the length of the maxilla lying dorsomedial to the alveolar portion anteriorly and superiorly adjacent to that portion (and hence flooring the niche) posteriorly. The niche opens medially into the elongate lateral chamber, which, in turn, opens posteriorly into the nasal cavity as in AM F.57844. At least one small opening perforates the ventral edge of the partition separating the lateral chamber from the nasal cavity. This thin partition inclines dorsolaterally at 30 degrees to the plane of the palate.

Similar lateral chambers are present in the skulls of *Alligator mississipiensis, Crocodylus johnstoni, C. novae-guineae* and *C. porosus,* although the chamber is much reduced in *C. johnstoni* relative to the others. The niche surmounting the alveolar portion of the maxillary wall is absent in these forms, and thus is presumably related to the snout depth of *Quinkana.* Apparently the maxillary wall is deeper than need be to accommodate the roots of the teeth, and a similar, but more marked condition is present in *Sebecus icaeorhinus.*

The anterior margin of the palatal fenestra is present, and is bounded dorsally by a curved rim, as in AM F.57844. The contact surfaces for the palatines indicate that these elements dorsally overlapped the palatal portions of the maxillae, again as in AM F.57844.

A ziphodont crown is preserved in the fifth alveolus from the front: it is serrate posteriorly, but no serrations could be seen on the poorly preserved anterior margin. The isolated crown likewise is serrate posteriorly but obscured anteriorly. The delicate state of the specimen precludes any further preparation of either tooth for the present.

The form and orientation of the alveoli, and the presence and form of the partition anteriorly rimming the palatal fenestra indicate reference to *Quinkana.* But the specimen is too incomplete for assessment of its specific allocation, and will be referred to *Quinkana* sp. Its smaller size and relatively thinner bone suggest a juvenile individual. The presence of a ziphodont tooth *in situ* in the left maxilla supports the inference that the type specimen of *Q. fortirostrum* also possessed a ziphodont dentition.

THE CROYDON SPECIMENS: At "Alehvale" Station, near Croydon, north Queensland, Archer collected three isolated ziphodont crowns (QM F.9220, QM F.9225 and QM F.9226) in 1976, and two fragments of maxilla, each with a single ziphodont tooth *in situ,* in 1977 (QM F.10141). All specimens were collected from the top of the wall of a dam constructed on "Alehvale". During excavation for the construction of the dam, fossil crocodilian material was reportedly encountered 6 to 12 metres below ground level.

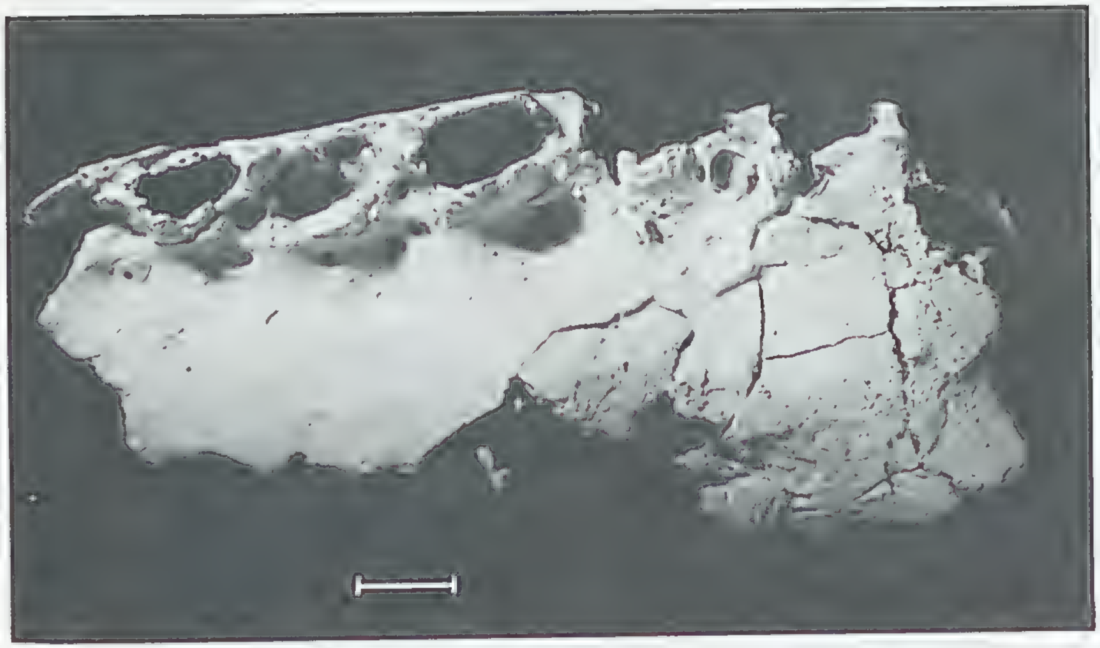


Fig. 8. *Quinkana* sp., QM F7898. Snout in ventral aspect. Scale 1 cm.

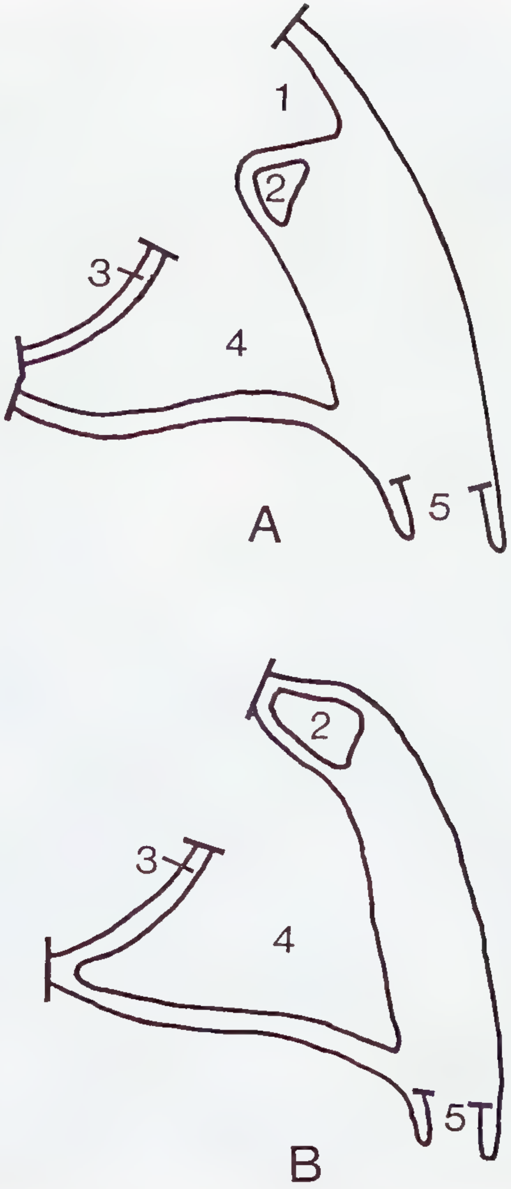


Fig. 9. Diagrammatic cross-sections of the snout of *Quinkana* sp., QM F7898. **A.** section at level of the first preserved maxillary alveolus, **B.** section at fourth preserved maxillary alveolus. Labels: **1.** niche dorsal to alveolar part of wall, **2.** narrow chamber between niche and alveolar part of wall, **3.** partition dividing nasal cavity from lateral chamber, **4.** lateral chamber, **5.** alveolus. Scale 1 cm.

Most of this material appeared referable to *Crocodylus* or some closely related genus (Archer, pers. comm., 1978). The occurrence near the top of the dam suggests that the ziphodont crocodilian material was encountered near the bottom of the excavation.

Both maxillary fragments represent the extreme posterior ends of that element, the more complete from the left side and the other from the right. Comparison with the corresponding portions of the maxillae of AM F.57844 has revealed differences of proportion, but from so few and incomplete specimens the significance, if any, of this variation cannot be determined.

The crown present in the right fragment is more compressed than most of the isolated crowns from this locality (Table 2), and is medially flexed. Without a complete tooth row the import of this change in crown form cannot be assessed. This tooth also shows a shallow, vertical sulcus in the medial surface of the root (also found in teeth of a ziphodont crocodilian from the Paleocene of New Mexico, UCMP 100029). Such sulci have been thought to be characteristic of theropod teeth, and absent in those of crocodilians (cf. Langston, 1956). The tooth tip is well worn, and gives the appearance that the tip was broken off prior to the wear.

THE "ROSELLA PLAINS" AND OTHER NORTH QUEENSLAND TEETH: Two isolated teeth (AM F.25227 and AM F.25228), found while excavating a well at "Rosella Plains" Station, north Queensland, were figured and described by Anderson (1930) as *Megalania* teeth. Hecht (1975) recognised these as crocodilian. Another ziphodont crown (QM F.1515) was received with teeth assigned by Longman to *Crocodylus nathani,* from the head of Tara Creek, near "Maryvale", north Queensland. This material may be Pliocene in age (Archer, pers. comm. 1978). None of the *C. nathani* type material appears to be distinct from the corresponding elements of *C. porosus,* so it is unlikely that this tooth derives from *C. nathani*. Two more teeth (QM F.10507) have recently been found at "Glen Garland" Station, central Cape York Peninsula (Fig. 14). All teeth closely resemble those from Croydon.

TABLE 2. Ziphodont teeth from Croydon

| Specimen | Maximum length of crown (L) | Maximum width of crown (W) | W/L | Serrations per 5 mm | |
|---|---|---|---|---|---|
| F9220 | 16.0 | 10.3 | 0.64 | 18 ant. | 19 post. |
| F9225 | 11.6 | 7.2 | 0.62 | 27 ant. | worn |
| F9226 | 12.9 | 7.1 | 0.55 | worn | worn |
| Right maxillary | 8.0 | 4.3 | 0.54 | 25 ant. | 27 post. |

THE DARLING DOWNS TEETH: Ziphodont crowns have also been collected from Pliocene deposits of the western Darling Downs (Fig. 13), at Chinchilla (QM F10204, QM F10205), as well as from Pleistocene deposits of the eastern Darling Downs, at Westbrook or Gowrie Creek (Toowoomba) (AM F.2876). These teeth, like those from north Queensland, are not sabre-like in form as are those from Pliocene of South Australia reported by Hecht and Archer (1977).

THE CHINCHILLA JUGAL: An isolated crocodilian jugal (Figs 11 and 12) from the Pliocene deposits at Chinchilla (QM F1152) bears sculpture much like that of the maxillae of the type of *Q. fortirostrum*. This jugal is very deep, much more so than that of *Crocodylus*. As discussed previously, the jugal of *Quinkana* must also have been deep,

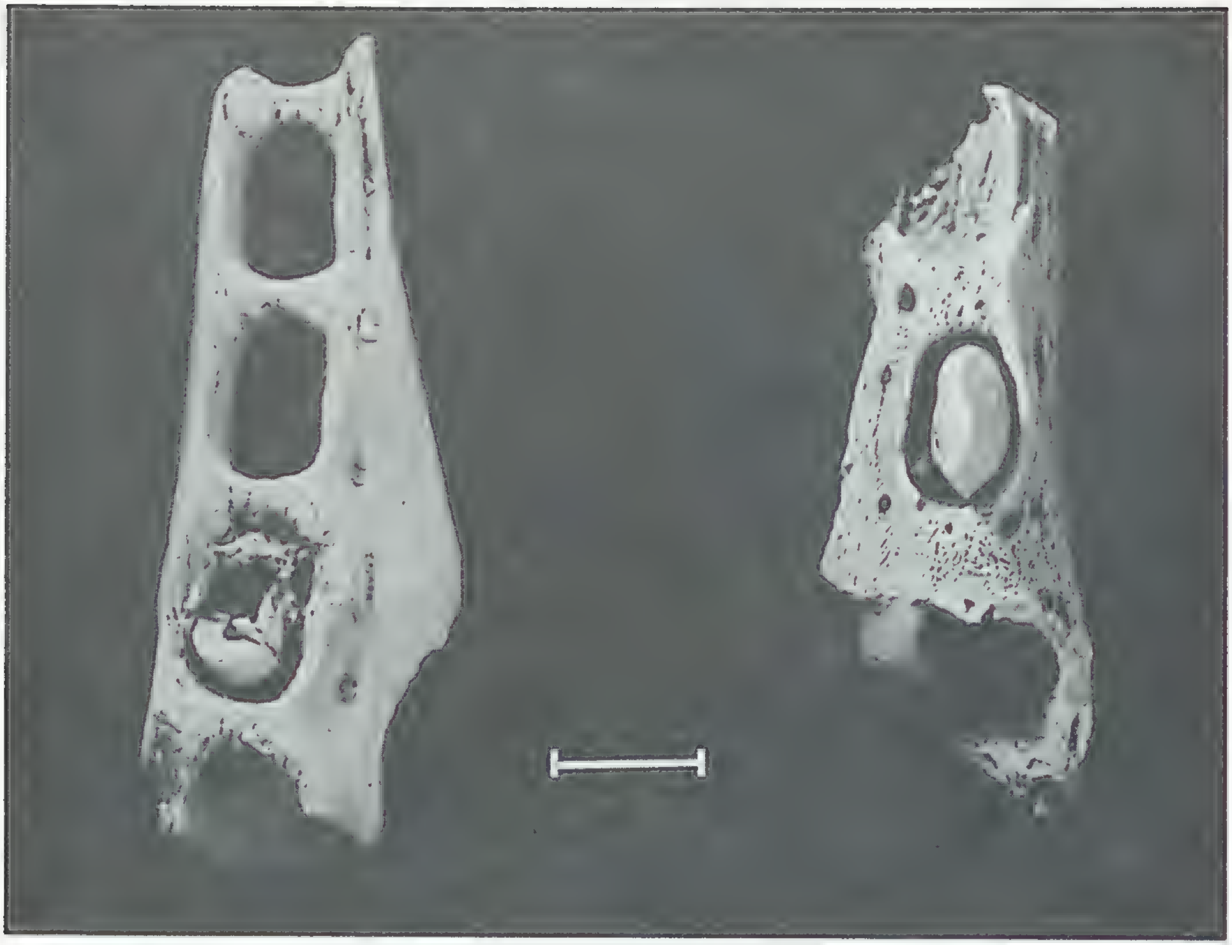


Fig. 10. Two fragments of the maxillae of a ziphodont crocodilian from near Croydon, north Queensland, QM F10141 in ventral view. Scale 1 cm.

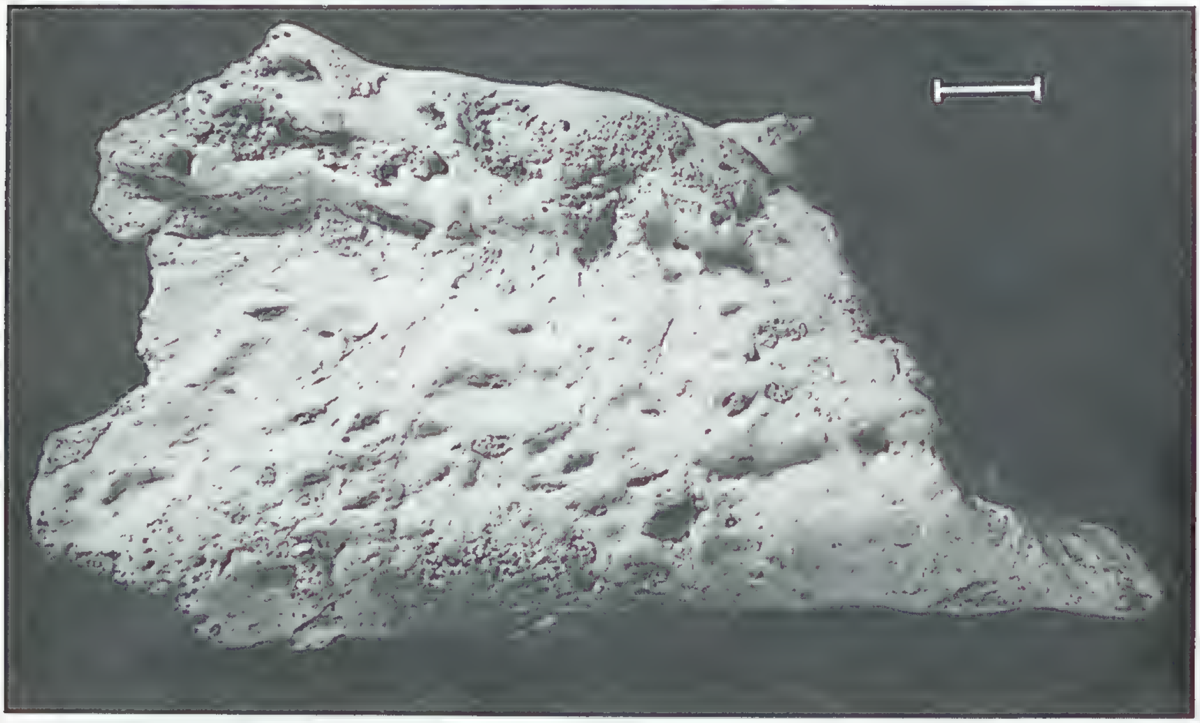


Fig. 11. Crocodilian jugal, QM F1152, from Chinchilla, in lateral view. Scale 1 cm.

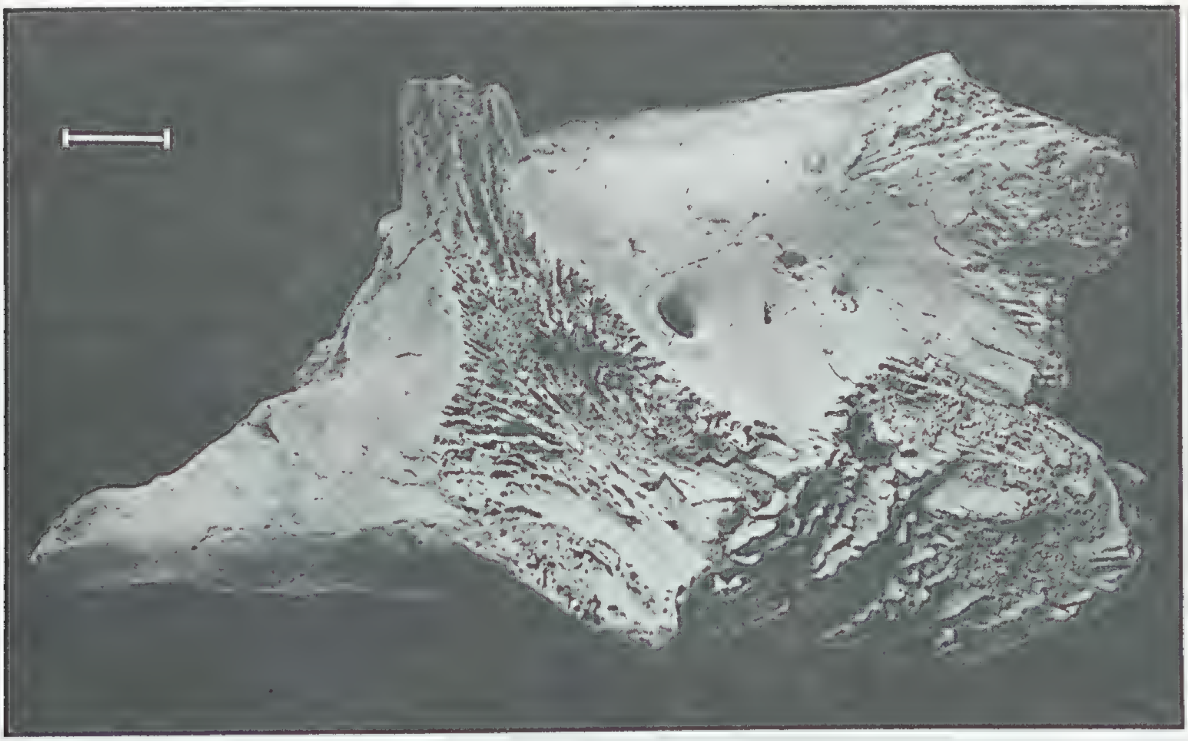


Fig. 12. Crocodilian jugal, QM F1152, from Chinchilla, in medial view. Scale 1 cm.

and the Chinchilla jugal would agree in size and in such proportions as can be deduced with what would be expected of *Quinkana*.

Ventrally the sculptured external surface is flexed to face downwards. Thus a ventral surface, reminiscent of the pitted ventral surface of the jugals of *Alligator mississipiensis*, but unlike those of any Australasian species of *Crocodylus*, was present. The postorbital bar is inset from the lateral surface, which bears a deep, longitudinal sulcus below the inferior orbital margin. The posterior process is unusually short and slender compared to the suborbital portion of this element (Fig. 11).

## CHARACTER ANALYSIS

CHARACTERS USED: The characters used to analyse the taxonomic relationships of *Quinkana fortirostrum* have been grouped into three suites: first, those related to the ziphodont condition; second, those related to the sebecosuchian and eusuchian conditions (i.e. infraordinal characters), and; third, a miscellaneous suite. The system of Hecht (1976) and Hecht and Edwards (1976) has been used as a guide in assessing the significance of these characters. These workers have divided all possible character states into five classes. These are:

I. Shared, derived states that result from loss.
II. Shared, derived states that result from simplification or reduction of complex structures.
III. Shared, derived states that result from age or size dependent processes, such as growth.
IV. Shared, derived states that make up some functional complex. These would be highly integrated and co-evolving.
V. Derived states "that are unique and innovative in determining new dichotomies and lineages" (Hecht, 1976, p. 344).

The states of these characters for thirty-four crocodilian genera, determined from the literature and available specimens are presented in Table 4. This information has been

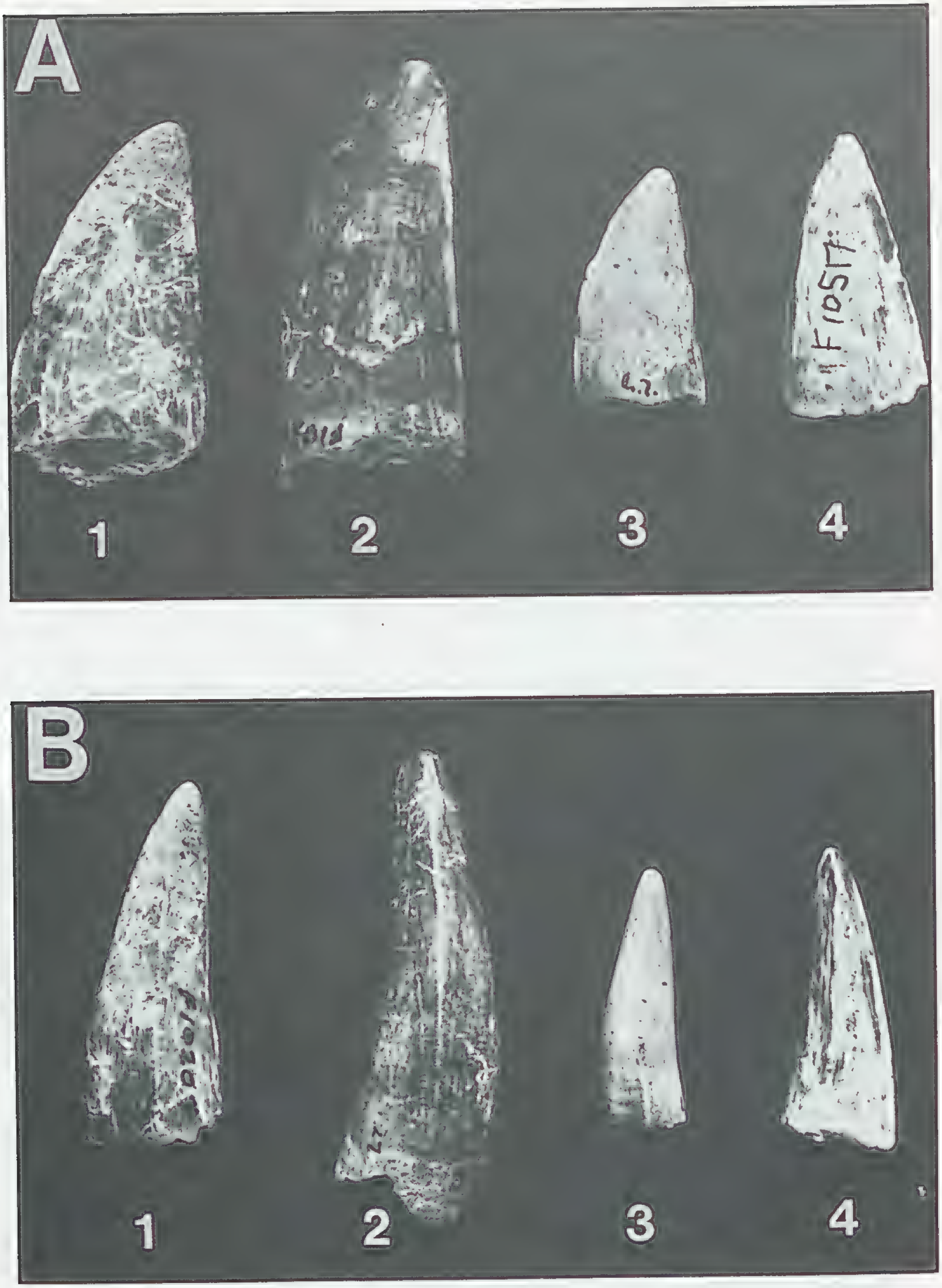


Fig. 13. Four isolated ziphodont teeth in lateral view (A) and anterior or posterior view (B). 1, QM F10204; 2 and 3, QM F10205, all three from Chinchilla, and; 4, QM F10517, from "Glen Garland". Scale 1 cm.

used to determine plesiomorphic states, based on the commonality of the state except where otherwise noted.

The first suite of characters, falling into Hecht's group IV (characters participating in an adaptive complex), clearly indicates the reference of *Quinkana* to the ziphodont crocodilians, but does not differentiate between the sebecosuchian and pristichampsine ziphodonts.

1. Snout depth. Crocodilian snouts are here arbitrarily classified into three categories of depth: low, those with a depth by width ratio (Table 3) less than 0.5; moderately deep, those for which this ratio is greater than or equal to 0.5 and is less than 1.0; and deep, those for which this ratio is greater than or equal to 1.0. Both this set of terms and those introduced for snout breadth agree with general usage. Low snouts are plesiomorphic for both mesosuchians and eusuchians.

2. Snout breadth. Crocodilian snouts are also here classified into three categories of breadth: broad, those with a length by breadth ratio (Table 3) greater than or equal to 0.66; moderately narrow, those in which this ratio is less than 0.66 and greater than 0.33; and narrow, those in which this ratio is less than or equal to 0.33. The broad snout is here considered plesiomorphic, although it is recognised that narrow snouted marine crocodilians, such as the teleosaurs, occur as early or earlier in the fossil record than broad snouted forms. These forms are not ancestral to later broad snouted taxa however and are usually considered specialised for a marine existence (cf. Kälin, 1955; Langston, 1973; Steel, 1973).

The genus *Crocodylus* includes species (e.g. *C. cataphractus* and *C. johnstoni*) with narrow snouts, suggesting that snout breadth considered in isolation might be regarded as variable. Among ziphodont crocodilians, however, snout breadth usually correlates with the presence of a ziphodont dentition and with snout depth. Non-Australian ziphodont crocodilians have narrow to moderately narrow deep to moderately deep snouts (cf. Berg, 1961; Langston, 1975).

3. Maxillary wall inclination. The inclination of the maxillary wall is related to the breadth and depth of the snout, narrow, deep snouts having a steep inclination, while low, broad snouts have a shallow inclination. For intermediate conditions, for example, a moderately deep, moderately narrow snout, variation in inclinations is conceptually possible. Since both low and broad snouts are plesiomorphic, it follows that shallow inclinations are also plesiomorphic. Only one non-ziphodont crocodile, of the thirty-four crocodilians for which information was available, shows a steep inclination, and that is *Paleosuchus palpebrosus*.

4. Dorsal margin of snout. All ziphodont crocodilians hitherto known possess a straight or slightly convex dorsal margin to the snout. Almost all other crocodilians have a dorsal margin concave in lateral view, and thus this condition is taken as plesiomorphic.

5. Laterally compressed dentition. The term ziphodont refers to crocodilian teeth that are laterally compressed and serrate. Because some crocodilian teeth are serrate but not laterally compressed these traits will be treated as two separate characters. It should be noted that some crocodilians (e.g. *Uruguaysuchus*) have laterally compressed teeth that are not ziphodont. But such brevirostrine crocodilians are unlike any known ziphodont crocodilians. The plesiomorphic condition is a tooth of sub-circular or oval cross-section.

6. Serrations. Other than among ziphodont crocodilians, the only dental serrations known to me among crocodilians occur in large teeth of rounded cross-section referred

TABLE 3. Characters and character states.

| | Character | Character states | Condition |
|---|---|---|---|
| 1 | Snout depth | low<br>moderately deep<br>deep | plesiomorphic<br>apomorphic<br>apomorphic |
| 2 | Snout breadth | broad<br>moderately narrow<br>narrow | plesiomorphic<br>apomorphic<br>apomorphic |
| 3 | Maxillary wall inclination | shallow<br>steep | plesiomorphic<br>apomorphic |
| 4 | Dorsal margin snout | straight<br>concave dorsally | apomorphic<br>plesiomorphic |
| 5 | Lateral compression of teeth | present<br>absent | apomorphic<br>plesiomorphic |
| 6 | Serrations of teeth | present<br>absent | apomorphic<br>plesiomorphic |
| 7 | Relation of tooth rows during closure | lower medial to upper<br>interlocking | plesiomorphic<br>apomorphic |
| 8 | Enlarged maxillary alveoli | present<br>absent | plesiomorphic<br>apomorphic |
| 9 | Festooning | present<br>absent | plesiomorphic<br>apomorphic |
| 10 | Maxillary tooth count | less than 12<br>12-15<br>greater than 15 | apomorphic<br>plesiomorphic<br>apomorphic |
| 11 | Positions of nasals | dorsal<br>dorsolateral (nasal crest) | plesiomorphic<br>apomorphic |
| 12 | Nasal form | flared posteriorly<br>tapered posteriorly | plesiomorphic<br>apomorphic |
| 13 | Posterior process of premaxilla | present<br>absent | plesiomorphic<br>apomorphic |
| 14 | Post-fenestral alveoli | present<br>absent | apomorphic<br>plesiomorphic |
| 15 | Lachrymal-prefrontal knobs | present<br>absent | apomorphic<br>plesiomorphic |
| 16 | Anterior process of palatine | present<br>absent | plesiomorphic<br>apomorphic |
| 17 | Palatal premaxillary-maxillary contact | angulate<br>non-angulate | apomorphic<br>plesiomorphic |
| 18 | Antorbital portion of jugal | present<br>absent | plesiomorphic<br>apomorphic |

(dubiously) to *Pallimnarchus*. Thus the non-serrate condition is taken to be plesiomorphic.

7. Relation of tooth rows during closure. As among alligatorines, in ziphodont crocodilians the lower tooth row lies medial to the upper when the mouth is shut. This is presumably related to the efficiency of shearing, necessitating the passage of one tooth row past the other. The condition of crocodylines in which the teeth interlock is usually assumed to be primitive, although this condition is less widespread than that of the medial lower tooth row. The "overbite" of alligatorines is thus here taken as plesiomorphic.

8. Single or few enlarged maxillary alveoli. Most eusuchians and non-marine mesosuchians possess one or two enlarged maxillary teeth (and hence alveoli), usually the fourth, fifth or sixth maxillary teeth. Longirostrine forms, especially marine forms, have teeth of nearly equal size throughout the anterior part of the tooth row, gradually decreasing in size posteriorly. This tendency also appears among ziphodont crocodilians, and may be related to the shearing action of the dentition. The possession of one or two enlarged maxillary teeth is considered plesiomorphic.

9. Festooning. Festooning, resulting in a vertically undulating tooth row, might also interfere with the shearing action of the dentition. Colbert (1945) related differences in form of the jaw margins and their relation to the quadratomandibular articulation between theropod and hadrosaurid dinosaurs to the shearing and "nutcracker action" occurring with the closure of the jaws. A working model of the skull and jaws of *Crocodylus rhombifer*, showed that marked festooning results also in "nutcracker action" over much of the tooth row (although some shear does occur). During "nutcracker action" upper and lower teeth come together almost simultaneously, while during shear the point of contact of the upper and lower tooth rows travels anteriorly along these rows during closure. A similar model of the skull of *Sebecus icaeorhinus*, where the ventral margin of the maxilla forms a single convex curve, shows that the amount of tooth row involved in shearing is increased. Only the premaxillary teeth, which are not ziphodont, show "nutcracker action". Thus to increase shearing action festooning would be suppressed.

These characters constitute the first suite, probably related to the presence of a ziphodont dentition. Certain other characters, such as the alveolar process, which might also have been included were not used because of absence of relevent information in the literature. As shown in Table 4 there is independent variation among the states of these characters, not all occurring together in each taxon hence the characters are treated as independent in this analysis. Closure of the lower teeth medial to the upper tooth row, loss of an enlarged maxillary tooth (or teeth) and reduction of festooning may reasonably be related to increased efficiency of shearing action of the teeth.

Character 9 points up an ambiguity in the use of the scheme of weighting proposed by Hecht (1976). The state present in ziphodont crocodilians is clearly the loss of festooning, and hence would fall in Hecht's group I (losses) and thus render minimal phylogenetic information. Nonetheless, as demonstrated previously, this loss is part of the development of "a highly integrated functional complex" (Hecht and Edwards, 1976), and thus falls into group IV, which is considered of "great information content if properly evaluated" (Hecht, 1976). The problem is that a given character state may fall into more than one category, and that no priority of categories is presented. I shall here consider that such states are not simply losses and shall count them as falling into group IV.

The second suite of characters is:

10. Maxillary tooth count. A relatively low count of 12 to 15 maxillary teeth is plesiomorphic for mesosuchians and eusuchians (*vide* Table 4), although some genera of both groups have more. All known sebecosuchians (and notably *Baurusuchus)* have fewer than 11 maxillary teeth, and this low count is apparently apomorphic. This state distinguishes sebecosuchians from pristichampsines, which have at least 12 maxillary teeth.

11. Position of nasals. Sebecosuchians are distinguished by the possession of a nasal crest (Colbert, 1946), by virtue of which the nasals are broadly visible in lateral aspect. The plesiomorphic condition, found in other crocodilians, restricts the nasals to the dorsum of the snout.

12. Nasal form. Sebecosuchians and non-marine mesosuchians, have nasals that flare posteriorly. The majority of eusuchians have nasals that taper posteriorly: only the aberrant *Mourasuchus* departs from this condition. Since eusuchians derive from mesosuchians, the mesosuchian condition, i.e. flaring nasals, is here taken to be plesiomorphic, even though it is not the most widespread character state.

13. Posterior process of premaxilla. Most eusuchians and many mesosuchians have a short process projecting posteriorly from the premaxilla on the dorsum of the snout. This process separates the anterior portion of the nasals from the anterior portion of the maxillae. It is lacking in few crocodilians (among them the Sebecosuchia) and this absence is taken as apomorphic.

14. Relation of maxillary tooth row to palatine fenestra. All eusuchians known to me have a maxillary tooth row that extends well posterior to the front of the palatine fenestra. This condition is unknown among sebecosuchians and non-marine mesosuchians (excepting *Eutretauranosuchus*).

Characters 10, 11 and 13 have unique states among the sebecosuchians, while characters 12 and 14 have unique states among the eusuchians. Thus this suite of characters is useful in determining the infraordinal allocation of *Quinkana*.

The third suite of characters is:

15. Lachrymal-prefrontal knobs. These knobs are found only in *Quinkana,* and thus are autapomorphic (and perhaps variable from individual to individual). The lachrymal knobs may be related to the lachrymal ridges of *Crocodylus porosus* but, as all autapomorphs, reveal nothing about the taxonomic relations of *Quinkana*.

16. Anterior process of palatine. Except for *Brachyuranochampsa* and *Quinkana,* eusuchians, mesosuchians and sebecosuchians all have an anterior process of the palatine. Hence the presence of the process is considered plesiomorphic.

17. Form of premaxillary-maxillary contact on palate. *Quinkana* shows an unusual form of palatal premaxillary-maxillary contact. Only *Brachyuranochampsa, Kentisuchus* and *Osteolaemus* also show a U- or V-shaped contact of similar form, and in *Osteolaemus* this seems to be variable (cf. Kälin, 1933, with Wermuth and Mertens, 1961). The sporadic, non-systematic appearance of this character suggests that it is best considered apomorphic, appearing independently in several lines.

18. Relation of anterior margin of jugal to that of orbit. *Quinkana* again differs from almost all other crocodilians in that the jugal cannot have extended anterior to the front of the orbit. This condition is also found in *Paralligator* and *Osteolaemus,* and, for the

same reasons as given for character 17, is considered autapomorphic.

RESULTS OF ANALYSIS: Using the characters listed in Table 3, *Quinkana* was compared wth those genera previously determined to most closely resemble it (Molnar, 1977), and being sufficiently complete for comparison. The character states of *Sebecus, Pristichampsus, Quinkana, Paleosuchus* and *Osteolaemus* are given in Table 4. Many characters used to differentiate eusuchians from mesosuchians and sebecosuchians are not included because they are restricted to the postorbital region of the skull, not preserved in any known material of *Quinkana*.

*Quinkana* agrees with *Sebecus* in seven of the eighteen states (all of which are apomorphic states associated with the ziphodont condition), with *Pristichampsus* in ten of the eighteen, and with *Paleosuchus* and *Osteolaemus* in seven of the eighteen. Four of the states in which *Quinkana* agrees with *Pristichampsus, Paleosuchus* and *Osteolaemus* are apomorphic eusuchian states.

The seven states in which *Quinkana* agrees with *Sebecus* are all related to trophic adaptation and thus fall into Hecht's group IV (co-evolving, functionally integrated states). Of the ten states shared with *Pristichampsus* six are ziphodont adaptations, and fall into group IV, while the other four are derived states shared with the other eusuchians. The state of character 14, concerning the extension of the tooth row posterior to the front of the palatine fenestra, seems likely related to the development of the trophic apparatus (although not a part of the ziphodont adaptation), and hence may be put into group IV. The other three states do not obviously fall into any of Hecht's categories. The dorsal position of the nasals (character 11), the posterior taper of the nasals (character 12), and the posterior process of the premaxilla (character 13) do not seem to be losses (group I) or reductions (group II). Perhaps one could stretch a point and regard the tapered nasals as a reduction of flared nasals. But one could equally regard this as an increase in relative size of the lachrymals, and thus not a reduction at all. None of these states obviously falls into the category of highly integrated, coevolving functional complexes (group IV) and cannot fall into group V (which are derived but not shared character states), and thus seem by default to fall into group III. Since all character states would seem to be the result of allometric or other ontogenetic processes it would appear that any shared, derived state could fall into this group. Considering these states to fall in group III, the four states shared with *Pristichampsus* (and other eusuchians) carry sufficient import to determine that *Quinkana* is an eusuchian.

These states are also the majority of states by which *Quinkana* agrees with *Paleosuchus* and *Osteolaemus*. Of the other two such states, one is uncommon and variable (character 17, form of palatal maxillary-premaxillary contact) and thus considered to have been independently derived, and the other (character 2, snout breadth), although part of the feeding mechanism, appears to be part of two different adaptive complexes in the different forms. The broad snout of *Osteolaemus* and *Paleosuchus* is not related to any other ziphodont features in those forms, while *Quinkana* is admittedly the only ziphodont crocodilian to have a broad snout. The absence of any other features in common, however, compels abandonment of any hypothesis that *Quinkana* was an aberrant alligatorine that developed the ziphodont habitus independently of the other ziphodont crocodilians. Thus the application of Hecht's method supports the assessment of *Quinkana* as a crocodylid.

DISCUSSION OF ANALYSIS: The first suite of nine characters are all related to the ziphodont condition, and thus corroborate the suggestion that *Quinkana* was a ziphodont crocodilian. Each of these states falls into Hecht's group IV which he considers as quite informative. But care must be taken with this kind of analysis, as Hecht himself comments, for *Sebecus* and *Pristichampsus* agree in almost as many characters (nine out of eighteen) as *Quinkana* and *Pristichampsus* and of the former pair each belong to different infraorders. Such characters can be misleading if, as here, they pertain to adaptive complexes evolving independently, but which because of the environmental constraints and selection for optimal function come to closely resemble one another. If there is only one optimal way to do something, all optimal structures developed will closely resemble one another. The classical example of this is streamlining in large, fast-swimming fish, ichthyosaurs and cetaceans. In the example discussed here the effect is emphasized by the absence of postorbital and postcranial characters from the analysis.

Characters 8 and 9 which have shared states between *Quinkana* and *Sebecus,* but not between *Quinkana* and *Pristichampsus,* I regard as indicating no closer relationship of *Quinkana* to *Sebecus* than to *Pristichampsus. Quinkana* shares four of the five eusuchian character states with *Pristichampsus,* and none with *Sebecus.* (Obviously: had *Sebecus* these states it would be considered a eusuchian.) This indicates that *Quinkana* was a eusuchian, and a later one than *Pristichampsus* (cf. Molnar, 1978), and hence could have evolved a more efficient feeding mechanism than *Pristichampsus.* These differences cannot be taken at face value.

Since the states of the second suite are common to most eusuchians it is neither surprising nor indicative of special affinities that *Quinkana* also shares four of the five states with *Osteolaemus* and *Paleosuchus.*

The first suite of characters indicates that *Quinkana* is ziphodont, and the second that it is eusuchian. The third suite is those diagnostic of the genus *Quinkana.* Only one state present in *Quinkana* is shared with any of the other taxa used in the comparison, the angulate form of the palatal premaxillary-maxillary suture, shared with some specimens of *Osteolaemus tetraspis.*

All previously known ziphodont eusuchians (i.e. *Pristichampsus*) are classified in the subfamily Pristichampsinae Kuhn, 1968. Kuhn's definition of the subfamily, translated from the German and with description of the postcranial character states omitted, reads:

> For the narrow- and long-snouted genera *Pristichampsus* and *Weigeltisuchus,* that according to Berg are very probably synonymous, I suggest this new subfamily. The teeth are unmistakably dinosaur-like, compressed, with anterior and posterior serrations, (and) shearing bite; eusuchian . . . From the position of the fourth dentary tooth (it is) a crocodyline, from which it diverges in bite and tooth form. The teeth of the lower jaw bite lingual to those of the upper. (Kuhn, 1968, p. 40).

Of the four character states distinctive of pristichampsines given, *Quinkana* probably possessed two: it did not have a long nor a narrow snout. Because no other eusuchians are ziphodont and because *Quinkana* probably was, I consider that *Quinkana* probably will prove, when more material is found, to belong to this subfamily.

## COMMENTS ON OTHER ZIPHODONT CROCODILIANS

In view of the unexpected geographic and temporal occurrence of *Quinkana,* some comments on the palaeozoogeography and taxonomy of ziphodont crocodilians are in order. Langston (1956, 1975) has long worked in this area, and recently Buffetaut (1978) and Molnar (1978) have offered short reviews of ziphodont crocodilian palaeogeography.

In spite of the description of thirteen nominate genera of ziphodont crocodilians (not all here considered valid), only four genera are represented by material more complete than that known for *Quinkana*. These genera are *Baurusuchus, Hsisosuchus, Pristichampsus (= Limnosaurus* Marsh, *non* Nopcsa = *Planocrania = Weigeltisuchus)*, and *Sebecus*. The others *(Bergisuchus, Cynodontosuchus, Doratodon, Iberosuchus* and *Ilchunaia)* are represented by less complete material.

*Hsisosuchus chungkingensis* (Young & Chow, 1953) is the sole species of a monotypic family usually considered to be mesosuchian (e.g. Steel, 1973). Langston (1956) suggested that *Hsisosuchus* was an ancestral sebecosuchian, an interpretation that finds support in the presence of several apomorphic sebecosuchian character states, and the absence of any apomorphic non-sebecosuchian states. Like other sebecosuchians, *Hsisosuchus* has relatively few maxillary teeth (9 to 10), a nasal crest, and apparently lacks maxillary teeth posterior to the front of the palatal fenestra (Young and Chow, 1953, Fig. 7). *Hsisosuchus* differs from later sebecosuchians, such as *Sebecus,* in having a low, moderately broad snout. I interpret this as suggesting that the acquisition of a ziphodont dentition may have preceded the development of a laterally compressed, deep, narrow snout.

The occurrence of the earliest known, and structurally most primitive sebecosuchian in China, while most of the other taxa derive from South America, supports Langston's (1956) contention of a cosmopolitan sebecosuchian radiation. Since *Hsisosuchus* dates from the Jurassic, the possibility must be considered that sebecosuchian teeth have been collected from later Mesozoic beds and misidentified as theropod. The Cretaceous Austrian ziphodont *Doratodon carcharidens* is now considered to be closely related to *Hsisosuchus* (Buffetaut, 1979).

Buffetaut (1979) has argued that hsisosuchians constitute a third group of ziphodont crocodilians unrelated to sebecosuchians or pristichampsines. Buffetaut cites the greater compression of the teeth of hsisosuchians than of primitive members of the other groups as evidence for the absence of any close relation. However this may simply remove the two known hsisosuchian species from ancestry, but does not, I feel, eliminate some unknown hsisosuchian species from ancestry of the sebecosuchians: this unknown hsisosuchian would have to have retained a less-specialized dentition than *Hsisosuchus chungkingensis* or *Doratodon carcharidens.*

Much of the material currently referred to the Sebecosuchia is quite incomplete. While this material is clearly referable to ziphodont forms, its position in the Sebecosuchia is uncertain due to the absence of diagnostic characters in the material preserved. Such forms as *Bergisuchus* are best regarded as *incertae sedis.*

Molnar (1977), Hecht and Archer, (1977) and Buffetaut (1978b) showed that the monotypic genus *Planocrania* (Li, 1976) was not sebecosuchian. This genus lacks the nasal crest and maxillary tooth number of sebecosuchians, and shows a eusuchian palate (Li, 1976). No character states are reported in the type (and only described) specimen of *Planocrania datangensis* that are absent in the known species of *Pristichampsus* (Berg, 1966; Langston, 1975) and thus this species is to be regarded as *Pristichampsus datangensis,* new combination.

Hecht and Archer, (1977) suggest that the Palankarinna crocodile probably represents a sebecosuchian. *Quinkana* does not. Although it remains to be determined by what route sebecosuchians reached Australia (perhaps via Antarctica), pristichampsines would most likely have come from Asia. It is known that pristichampsines were spread throughout the northern hemisphere in the early Tertiary (Langston, 1956; Molnar, 1978), including south China (Li, 1976). Presumably like other forms that relatively recently reached Australia, they migrated through Indonesia and

New Guinea. The Otibanda teeth (which include no sabre-shaped crowns as are often found among sebecosuchians) may represent a vestige of this migration. The coexistence of sebecosuchians and pristichampsines would seem unusual, although this apparently occurred in Europe as well.

RANGE: Fossils of ziphodont crocodilians have been found in Queensland from central Cape York Peninsula in the north to the New South Wales border in the south. The sites fall into two groups (Fig. 14), one in the north and one in the south. Most of the localities are closely associated with the Great Dividing Range, with the exception of Croydon (at the end of the Gregory Range) in the north, and Chinchilla (on the Darling Downs) in the south. None of the localities is greatly removed from a modern watercourse, the most distant being Chillagoe which is approximately ten miles from the Walsh River, and through which runs a large creek. Croydon is also removed from a major modern watercourse, but there is geological evidence for a local watercourse at the time the fossils were deposited (Archer, pers. comm., 1978).

I feel that insufficient work on fossil crocodilians in Australia has been done to be sure that ziphodont crocodilians did not occur elsewhere. The collections of the Australian Museum and the Geological and Mining Museum in Sydney were searched for evidence of ziphodont crocodilians in New South Wales without success.

Although the evidence is scanty there is no suggestion of any change in range with time, as the Pliocene occurrences (Tara Creek and Toowoomba) are among both the northern and the southern group of sites.

ASSOCIATED FAUNAS: One of the localities that produced ziphodont teeth, "Rosella Plains" has yielded no other vertebrate remains. Each of the other localities has produced one or more additional tetrapod taxa. At "Glen Garland" teeth of three terrestrial mammals have been found with the ziphodont teeth. At Tara Creek and Croydon the ziphodont was found with remains referable to *Crocodylus porosus* or a very similar species. At Chinchilla a fauna of terrestrial mammals is known (Archer and Bartholomai, 1978), as well as at least two other forms of crocodile, currently under study, one of which is probably *C. porosus*. The Toowoomba area (Gowrie Creek especially) has produced a terrestrial Pleistocene fauna (Owen, 1877). At Texas Caves and Tea Tree Cave, faunas consisting largely of mammals have been found with the ziphodont crocodilians (Archer, 1978; Molnar, 1978). No other crocodilians were found at these localities, nor were other aquatic or amphibious forms represented.

Since the Queensland ziphodont crocodilians have been found both in association with apparently terrestrial faunas and with faunas that include amphibious elements, no conclusion as to the possible habitats of the ziphodonts themselves can be drawn from the faunal associations.

OCCURRENCE OF ZIPHODONT CROCODILIAN FOSSILS: The Chillagoe and the Texas Caves crocodile represent two of the few ziphodont crocodilian specimens that were found in cave deposits. The description of the deposits in The Joint at Texas Caves (Archer, 1978) describes equally well the deposits in Tea Tree Cave. There is some evidence that the bones in Tea Tree Cave all lie in one relatively narrow level, but this has yet to be confirmed.

The other Queensland ziphodont material was either collected from the surface (Chinchilla, Toowoomba and Tara Creek) or from excavations (Croydon, "Rosella Plains"). The environment of deposition of these latter sites has not been determined, although there is some suggestion that the Croydon material accumulated in the bottom of a stream channel or billabong (Archer, pers. comm., 1978).

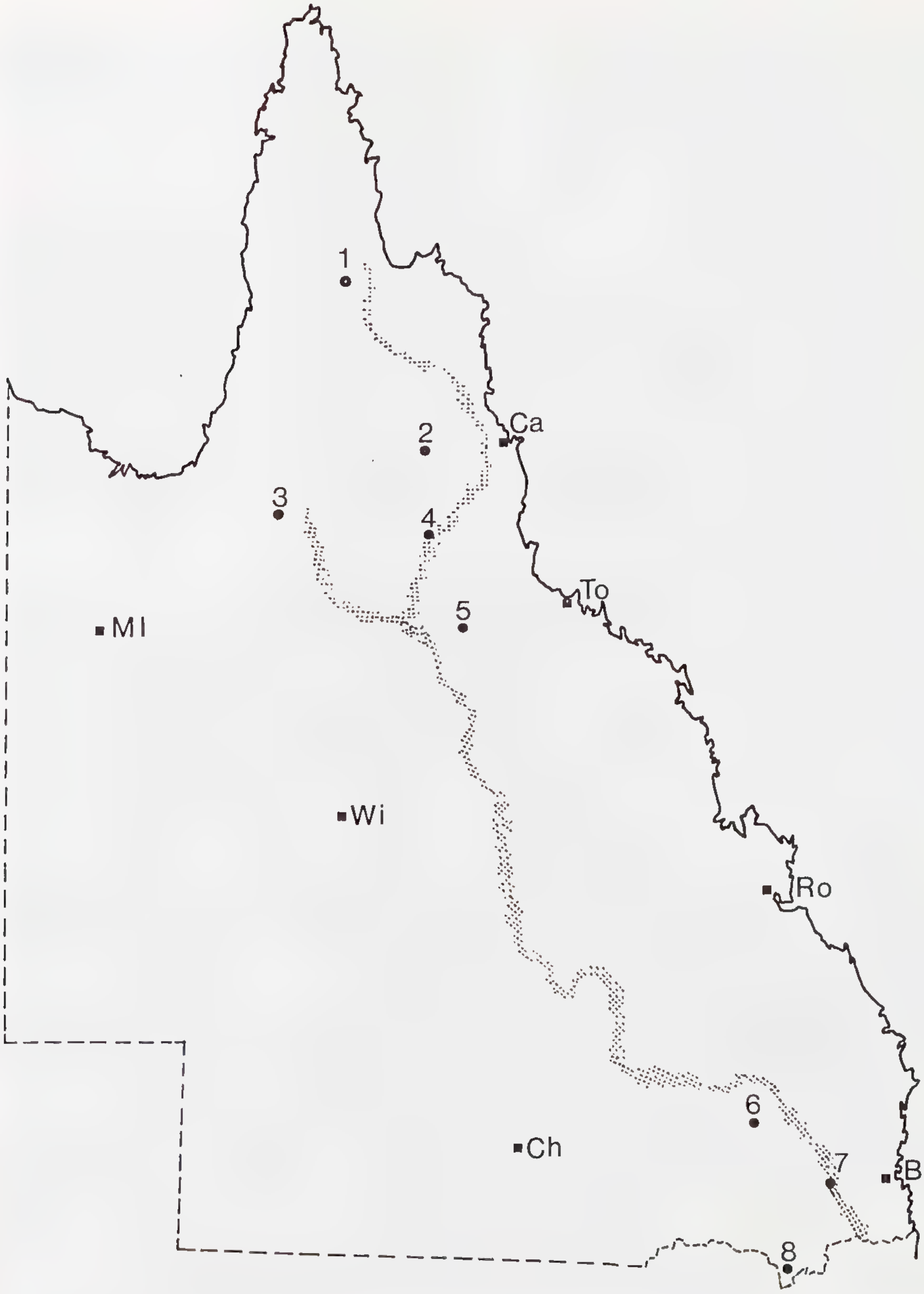


Fig. 14. Map of Queensland showing the distribution of known fossils of ziphodont crocodilians. 1, "Glen Garland"; 2, Chillagoe; 3, "Rosella Plains"; 4, Croydon; 5, Tara Creek; 6, Chinchilla; 7, Toowoomba; 8, Texas Caves; Br, Brisbane; Ca, Cairns; Ch, Charleville; MI, Mount Isa; Ro, Rockhampton; To, Townsville; Wi, Winton.

In view of the unusual occurrence of some of the Australian ziphodont material, and of the evidence suggesting terrestrial (as opposed to amphibious) habits of ziphodont crocodilians (Kuhn, 1938; Zappler, 1960), it is worth reviewing the conditions of deposition of beds bearing ziphodont crocodilian remains. Occurrences of isolated teeth will usually not be considered, because of the obvious possibility of transportation. The material is treated by continent.

South America. The type of *Sebecus icaeorhinus* derives from a pocket of the Casamayor Formation, associated with a fauna not elsewere found in that formation (Colbert, 1946). This fauna includes a waterbird, turtles and a frog and hence suggests a near-water environment. The second specimen of *S. icaeorhinus* was apparently a surface find deriving from beds of Casamayorian age yielding a typical *Notostylops* fauna (Colbert, 1946). The Brazilian *Sebecus* sp. derives from Paleocene fissure or cave fills of the Sâo José de Itaboraí Basin (de Paula Couto, 1953; Codevila Palma and Brito, 1974), but no further information is recorded. The type jaw of *Sebecus huilensis* derives from the La Venta fauna, from a unit ("Monkey unit") of the Honda Group (Langston, 1965). *Caiman neivensis* was also found at this locality, so a near-water environment is again possible. The Peruvian *Sebecus* cf. *S. huilensis,* from the Ipururo Formation is associated with a fauna containing turtles and other crocodilians (Buffetaut and Hoffstetter, 1977), suggesting a near-water environment.

*Cynodontosuchus rothi* derives from the "Estratos con Dinosaurios" (Upper Cretaceous) of Neuquen which has also produced a dinosaur fauna. *Ilchunaia parca* derives from the Divisadero Largo Fm. along with a fauna of snakes, turtles and various mammals (Báez and Gasparini, 1977; Simpson, Minoprio and Patterson, 1962). *Baurusuchus pachecoi* comes from the Baurú Series, which also yields the goniopholid *Itasuchus,* podocnemids, teleosts and fresh-water invertebrates (Price, 1955). Obviously this is an aquatic deposit: although no further stratigraphic details are given by Price (1945), Beurlen (1970) implies that *Baurusuchus* derives from the upper Baurú at Marilia, which he describes as "lacustrine-limnic".

North America. The principle specimens of *Pristichampsus vorax* come from the Washakie and Bridger Basins (Langston, 1975). In the Washakie Basin the Green River Formation is a well-known fresh-water deposit, while the Washakie Fm. is also fluvial (Black, 1967; Roehler, 1973). The Bridger Fm. is predominantly fluviatile, with a large number of thin layers of lacustrine sediments. Much volcanic ash apparently fell during the deposition of this formation (Bradley, 1964).

Europe. Both *Pristichampsus rollinati* and *Bergisuchus dietrichbergi* have been found in the Eocene near Messel, Germany, in association with much other crocodilian material (Berg, 1966). Matthess (1966) suggests a larger water system than presently exists, and gives evidence suggesting wooded or forested conditions.

*P. rollinati* has also been found in the Geiselthal deposits. These are described as having been deposited in a forest with river and ponds (Kurten, 1971) and in a swampy forest with open swampland (Zappler, 1960): both cases presenting a near-water environment.

*P. rollinati* and *Pristichampsus* sp. have also been reported in the Eocene of the Paris Basin and of southern France, and involve beds of fluvial or lacustrine origin, which have also yielded the remains of other types of crocodilians (Buffetaut, pers. comm., 1979). One tooth has been found in the phosphorites of Quercy (Berg, 1966), which are cave deposits.

*Doratodon carcharidens* from the Cretaceous Gosau Fm. of Austria derives from fresh-water beds (Bunzel, 1871; Suess, 1881). *Iberosuchus macrodon* occurs at widely distributed localities on the Iberian Peninsula (Antunes, 1975). Antunes (1975) concludes that "Sedimentological and other evidence concerning the localities strongly suggests that, . . . *Iberosuchus* would be less strictly aquatic dwellers than most Crocodilia. They may equally have frequented high energy water courses, . . ." (p.290).

Asia. No relevant information is yet available for *Pristichampsus datangensis*. *Hsisosuchus chungkingensis* was found associated with *Plesiochelys,* but no further details are available (Young and Chow, 1953).

Pristichampsine material (Buffetaut, 1978b) has also been recently described from what appears to be a portion of the Kuldana Fm., in Pakistan. This material occurs together with other crocodilian remains in fluviatile deposits (Buffetaut, pers. comm., 1979). Sahni, Srivastava and D'Souza (1978) have reported ziphodont teeth (that they attribute to a pristichampsine) from a calcareous shale in the Subathu Fm., of Jammu and Kashmir in northwest India. They suggest that the Indian ziphodonts were "river or river bank carnivores." Maw, Ciochon and Savage (1979) list ziphodont crocodilian remains (described as sebecid) from claystones in the Pondaung Fm. of Burma. From the same beds also come fish, turtles, other crocodilians, brontotheres, amynodonts and anthracotheres, so a subaqueous deposition of the beds is indicated.

In conclusion, there are only two known occurrences of ziphodont crocodilian fossils in caves, or fissure fills, other than in Queensland. Most, if not all other occurrences of ziphodont crocodilians are in deposits that formed under or near water. Hence there is no decisive indication of terrestrial habits for ziphodont crocodilians from the environments of deposition in which they were buried, nor any contradiction either, since most terrestrial tetrapods are buried in subaqueous deposits. The occurrence of some Australian specimens in caves strongly suggests that the crocodiles fell into the caves and died there. This, in turn, suggests that they wandered overland. Modern individuals of the genus *Crocodylus* however often wander overland some distance from water (Cott, 1961; Webb, pers. comm., 1978) so this does not constitute good evidence for terrestrial habits.

INFERRED HABITS OF AUSTRALIAN ZIPHODONT CROCODILES: None of the Australian ziphodont crocodilian material is sufficiently complete to allow any biomechanical analyses, so that any speculation of the habits of these crocodiles must be extrapolated from knowledge of the other, better known ziphodonts. On the basis of two features of the postcranial skeleton of "*Weigeltisuchus geiseltalensis*" (here considered a synonym of *Pristichampsus rollinati*), the hooflike unguals and the rounded, rather than laterally flattened, tail it has been suggested that this form was more terrestrial in habits than other crocodilians (Kuhn, 1938).

The discovery of the best two specimens of Australian ziphodont crocodilians in caves certainly does not contradict this, but neither (as previously noted) does it unambiguously support this suggestion. Nor does the occurrence of ziphodont crocodilians in the more usual kind of deposits shed light on this question.

The possession of ziphodont teeth and the associated lateral compression of the snout would seem to indicate predation upon larger prey than is usual for crocodilians, but does not indicate that this prey was terrestrial: they may have preyed upon other crocodilians, for example.

The relative absence of large terrestrial predators in the Tertiary and Pleistocene deposits of Australia (cf. Archer and Bartholomai, 1978, Fig. 2), other than the giant varanid *Megalania,* leads to the suspicion that the role of large terrestrial predator may have been played by the reptiles, specifically *Megalania* and *Quinkana.* Only further discoveries will demonstrate whether or not this interesting hypothesis can be supported.

## REVIEW

The Chillagoe crocodile, based on the rostral portion of a skull (AM F.57844), is described as the type specimen of the new genus and species, *Quinkana fortirostrum.* This species is characterised by a broad, moderately deep snout, a distinct alveolar process on the maxilla, the anterior process of the palatine very short or absent, and a jugal that does not project anterior to the orbit. The alveoli lie in a distinctive pattern and suggest the presence of ziphodont teeth. A second specimen (QM F7898), from Texas Caves, also referred to this genus, does have a single ziphodont crown *in situ.*

Ziphodont teeth have also been found isolated at "Alehvale" (with some cranial fragments), "Rosella Plains", "Glen Garland", and Tara Creek, in north Queensland, and near Chinchilla, and Toowoomba on the Darling Downs. An isolated, deep crocodilian jugal (QM F1152) found at Chinchilla may pertain to *Quinkana.*

A character analysis, modelled on the work of Hecht (1976) indicates the eusuchian nature of the specimen and suggests a relationship to *Pristichampsus.* Problems encountered in the use of this mode of analysis include ambiguity in the definition of the possible categories of character states, particularly in regard to losses or reductions, and discrimination of parallelism.

*Hsisosuchus chungkingensis* possesses several apomorphic sebecosuchian character states (few maxillary teeth, nasal crest, and absence of maxillary teeth posterior to the palatal fenestra) and is thus considered the oldest known sebecosuchian.

No information about ziphodont crocodilian habits can be drawn from stratigraphic occurrences, although the finding of the two most complete Australian specimens in caves suggested that at the very least they did wander overland.

## ACKNOWLEDGEMENTS

The specimens were kindly made available for study by Dr A. Ritchie of the Australian Museum, and Dr M. Archer of the Queensland Museum. Mr Alan Easton, Queensland Museum, produced the photographs used in Figs. 7, 8, 10, 11 and 12. Helpful in sundry matters were Mr R. Jones, and Drs M. Archer, E. Buffetaut, Z. B. Gasparini, W. Langston, Jr., T. H. Rich, and A. Ritchie. Mr T. Robinson and Mr L. Francis, of the Chillagoe Caving Club, provided invaluable assistance during the inspection of Tea Tree Cave. Mr R. Hawkins and Mr G. Middleton, of the Sydney Speleological Society, also provided noteworthy assistance. Miss J. Hamilton patiently typed the innumerable drafts of this paper.

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TABLE 4. Character States in Crocodilian Skulls. The following table enumerates the states of the eighteen characters used in the taxonomic analysis of *Quinkana fortirostrum*. This illustrates the commonality of the various characters, and was used to determine plesiomorphs and apomorphs.

The characters are designated by the same numbers used in the text. The genera included and the symbols used in the table are listed below. Two symbols separated by a slash indicates that both states are present in that genus.

List of symbols used in supplementary table.

For all characters:
? state not determinable from literature or specimens

For characters 5 to 9 and 13 to 18:
+ present
− absent

For character 1:
l low
md moderately deep
d deep

For character 2:
b broad
mn moderately narrow
n narrow

For character 3:
nh less than 45 degrees
nv greater than 45 degrees

For character 4:
s straight
c concave

For character 11:
d dorsal
dl dorsolateral

For character 12:
t tapered
f flared
o parallel

| | Character State | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Genus | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
| Mesosuchia | | | | | | | | | | | | | | | | | | |
| Atoposauridae | | | | | | | | | | | | | | | | | | |
| *Alligatorellus* | l | b | ? | s | – | – | ? | + | – | 13 | ? | t | ? | ? | – | ? | ? | ? |
| *Alligatorium* | ? | b | ? | ? | – | – | ? | ? | ? | ? | ? | t | ? | ? | – | ? | ? | ? |
| Goniopholidae | | | | | | | | | | | | | | | | | | |
| *Amphicotylus* | l | mn | nh | c | – | – | ? | + | + | 15 | d | f | + | – | – | + | – | + |
| *Eutretauranosuchus* | ? | mn | ? | ? | – | – | ? | + | ? | 18 | d | f | ? | + | – | + | ? | ? |
| *Goniopholis* | ? | mn/b | nh | ? | – | – | ? | ? | ? | ? | d | f | + | ? | – | + | ? | + |
| Paralligatoridae | | | | | | | | | | | | | | | | | | |
| *Paralligator* | l | b | nh | c | – | – | + | + | + | 14 | d | t | – | ? | – | ? | ? | – |
| Bernissartiidae | | | | | | | | | | | | | | | | | | |
| *Bernissartia* | ? | mn | ? | ? | – | – | ? | + | ? | 19/20 | d | ? | ? | + | – | ? | ? | ? |
| Sebecosuchia | | | | | | | | | | | | | | | | | | |
| Baurusuchidae | | | | | | | | | | | | | | | | | | |
| *Baurusuchus* | d | n | nv | s | + | + | + | + | – | 5 | d | ? | + | – | – | ? | ? | + |
| Sebecidae | | | | | | | | | | | | | | | | | | |
| *Sebecus* | d | n | nv | s | + | + | + | – | – | 10/11 | dl | f | – | – | – | + | – | + |
| Hsisosuchidae | | | | | | | | | | | | | | | | | | |
| *Hsisosuchus* | l | mn | ? | ? | + | + | + | + | – | 9 | dl | ? | ? | – | – | ? | ? | ? |
| Eusuchia | | | | | | | | | | | | | | | | | | |
| Nettosuchidae | | | | | | | | | | | | | | | | | | |
| *Mourasuchus* | l | mn | nh | c | – | – | + | ? | ? | ? | d | f | + | ? | – | ? | ? | + |
| Crocodylinae | | | | | | | | | | | | | | | | | | |
| *Asiatosuchus* | ? | b | nh | ? | – | – | + | + | ? | 14 | d | t | + | + | – | + | – | ? |
| *Brachyuranochampsa* | ? | mn | ? | ? | – | – | ? | + | ? | 14 | d | t | + | + | – | – | + | + |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Crocodylus* | l | n-b | nh | c/s | – | – | – | + | + | 14/15 | d | t | + | + | – | + | +/– | ? |
| *Kentisuchus* | l | n | ? | ? | – | ? | – | + | – | 15? | d | t | + | ? | – | ? | + | + |
| *Leidyosuchus* | l | mn | nh | c | – | – | – | + | + | 19/20 | d | t | + | + | – | + | – | ? |
| *Navajosuchus* | l | b | nh | c | ? | ? | ? | + | + | 14/15 | d | o | + | + | – | + | – | + |
| *Orthogenysuchus* | ? | mn | ? | ? | – | – | – | ? | ? | ? | ? | t | + | ? | – | ? | ? | + |
| Alligatorinae | | | | | | | | | | | | | | | | | | |
| *Albertochampsa* | l | b | nh | ? | – | – | ? | + | + | 15 | d | t | + | + | – | + | – | + |
| *Alligator* | l | b | nh | c | – | – | + | + | + | 12/14 | d | t | + | + | – | + | – | +/– |
| *Allognathosuchus* | l | b | nh | s | – | – | + | + | + | 13 | d | t | + | ? | – | ? | ? | + |
| *Brachychampsa* | ? | b | ? | ? | – | – | + | + | ? | 14 | d | t | + | + | – | ? | – | + |
| *Caiman* | l | mn/b | nh | c | – | – | + | + | + | 12/15 | d | t | +/– | + | – | + | – | + |
| *Ceratosuchus* | ? | b | ? | ? | – | – | + | + | ? | 14? | d | ? | ? | ? | – | + | ? | ? |
| *Diplocynodon* | l | b | nh | c | – | – | + | + | + | 16/17 | d | t | + | + | – | + | – | + |
| *Hispanochampsa* | ? | b | ? | ? | ? | ? | + | ? | ? | 16 | d | t | + | + | – | + | ? | + |
| *Melanosuchus* | l | b | nh | c | – | – | + | + | + | 13 | d | t | + | + | – | + | – | + |
| *Osteolaemus* | l | b | nh | c | – | – | – | + | + | 12/13 | d | o/t | + | + | – | + | +/– | – |
| *Paleosuchus* | md | mn/b | nv | c | – | – | + | + | + | 14/15 | d | t | + | + | – | + | – | + |
| *Procaimanoidea* | ? | b | ? | ? | – | – | + | + | ? | 13 | ? | t | + | + | – | +/– | – | + |
| *Prodiplocynodon* | l | b | nh | ? | – | – | ? | + | + | 13/14 | d | ? | ? | + | – | ? | ? | ? |
| Thoracosaurinae | | | | | | | | | | | | | | | | | | |
| *Maroccosuchus* | ? | mn | ? | ? | – | – | ? | ? | ? | ? | d | t | + | ? | – | ? | ? | + |
| Pristichampsinae | | | | | | | | | | | | | | | | | | |
| *Pristichampsus* | md | mn | nv | s | + | + | + | – | – | 13/16 | d | t | + | + | – | + | – | + |
| Subfamily incertae sedis | | | | | | | | | | | | | | | | | | |
| *Quinkana* | md | b | nv | s | + | + | + | – | – | 12 | d | t | + | + | + | – | + | – |

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## NOTE ADDED IN PROOF

An incomplete maxilla with two teeth *in situ* (QM F10771) was recently collected from "Glen Garland" Station. While generally agreeing with the maxilla of *Quinkana fortirostrum* in form and sculpture, and particularly in the presence of pits for the reception of the dentary teeth between the maxillary alveoli, this maxilla differs in alveolar form and orientation. This suggests either a second Pleistocene ziphodont taxon, or that *Q. fortirostrum* is quite variable in alveolar morphology. The "Glen Garland" ziphodont material, kindly brought to our attention by Mr D. Ree, occurs in association with *Megalania*, chelonian, macropod and diprotodontan material.

Submitted 10 April, 1979
Revised manuscript accepted for publication 3 June, 1980

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